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***Tetragonula* Stingless Bees of the Continental Asia and Sri Lanka (Hymenoptera, Apidae)^{1) 2)}**

By

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(With 124 Text-figures, 1 Plate and 36 Tables)

As in many animal groups, the Indomalayan stingless bees involve two types of species, those being easily distinguished from others and those not. Most species belong to the first type, for which the excellent papers by Schwarz (1937, '39) are still useful. But there are some species representing the second type which require critical studies. Most of these species belong to *Trigona iridipennis* complex or the subgenus *Tetragonula* (erected by Moure 1961 as a genus, cf. Sakagami 1975), which is, unfortunately, the largest and most widespread group in the Indopacific areas, including some commonest species. Moure (op. cit.) pointed out the necessity of a thorough restudy of the entire group. By this reason I excluded this group in my previous paper on the S.E. Asiatic stingless bees in the collection of Bernice P. Bishop Museum (op. cit.). Later, by the courtesy of many colleagues, I could examine a large number of additional materials, not only from S.E. Asia but also from India and Sri Lanka. Certain earlier ambiguities were solved but some "forms" which are difficult to accurately classify were newly obtained. Therefore, the present paper should be regarded as an interim report on this difficult group.

Tetragonula was precisely described and defined by Moure (1961). Some important features in workers are summarized:

1) Small to very small, body and wing (including tegula) length 2.5~4.5 mm. 2) Integument polished with fine punctures, not tessellate. 3) Clypeus without stout erect hairs. 4) Mandible bidentate. 5) Malar space much shorter than flagellar width. 6) Flagellomeres very short, shorter than width. 7) Mesoscutellum well projected backward, distinctly exceeding propodeum. 8) Marginal cell nearly closed apically. 9) Bifurcation of *M* and *Cu* nearly at *cu-an*. 10) Posterior fringe of hind tibia mostly plumose. 11) Hind tibia below with a moderately broad, raised and pubescent area. 12) Hind basitarsus narrower than tibia, below basally with a large sericeous area. 13) Propodeum medially

1) Contributions to the knowledge of the Indopacific stingless bees. II.

2) By inclusion of the Sinhalese materials, the present paper forms a part of "Biosystematic Studies of the Insects of Sri Lanka" directed by Dr. Karl V. Krombein, Smithsonian Institution, Washington, D.C.

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smooth and glabrous. 14) Metasoma flat, anterior terga polished.

Having synonymized many earlier names, Schwarz (1939) recognized seven forms in the continental Asia. Later Moure (1961) published his notes on the examination of type specimens of various forms without presenting his own system. The system by Schwarz and that adopted in the present paper are synoptically presented:

Schwarz	Sakagami
<i>melina</i> Gribodo	<i>melina</i>
<i>geissleri</i> Cockerell	<i>latigenalis</i> sp. nov.
<i>sarawakensis</i> var. <i>sarawakensis</i> Schwarz	<i>geissleri</i>
<i>iridipennis</i> var. <i>iridipennis</i> Smith (India)	<i>sarawakensis</i>
<i>iridipennis</i> var. <i>iridipennis</i> Smith (S.E. Asia)	<i>iridipennis</i>
<i>iridipennis</i> var. <i>valdezi</i> Cockerell	} <i>laeviceps</i> Smith
	<i>hirashimai</i> sp. nov.
	<i>zucchii</i> sp. nov.
	<i>gressitti</i> sp. nov.
	<i>pagdeniformis</i> sp. nov.
	<i>minor</i> sp. nov.
<i>fuscobalteata</i> var. <i>fuscobalteata</i> Cameron	<i>fuscobalteata</i>
<i>fuscobalteata</i> var. <i>pagdeni</i> Schwarz	<i>pagdeni</i>

The most important change concerns *T. iridipennis*, the type species of the subgenus. This species has formerly been regarded as very widespread from India to Solomon Is. The critical study has proved its confinement to India and Sri Lanka. For the populations of "*iridipennis*" by Schwarz in S.E. Asia, I adopt the name *T. laeviceps* proposed by Moure (1961). *T. iridipennis* thus redefined is structurally fairly distinct from *T. laeviceps*, rather being close to *T. pagdeni*, which is also considered an independent species, not a variety of *T. fuscobalteata*.

A few words are given as to the newly described species. Any revisional studies seek two aims, to find a consistent classificatory system and to give the appropriate name for each taxon recognized. Both are important but the present study mainly deals with the first aim. It is possible that some new species which were obliged to erect below are synonymous with some old names already synonymized by Schwarz. I welcome any attempts to elucidate such relations, provided the effort would be made on a sound basis. But some species are so variable in size and coloration that it will be difficult to obtain a reasonable conclusion from comparison of a limited number of museum specimens.

Specific characters

The main difficulty in sorting *Tetragonula* is the virtual absence of reliable structural characters in workers. Consequently the classification must depend on size, proportion, coloration and pilosity, which makes the identification of particular specimens difficult or often impossible. Males are more easily distinguished by

structural characters but they are poorly represented among museum specimens. Out of 13 species recorded below males are known only in eight. Some remarks are given on the characters adopted.

1. **Size:** Five characters were chosen: BL (body length) and WL₁ (length of fore wing including tegula,) HW (maximum head width), WL₂ (distance between *M-Cu* bifurcation and basal tip of marginal cell, cf. Fig. 1 below), HTL (distance between upper basal end to midpoint of apical margin of hind tibia, cf. Fig. 2 below). The first two are convenient to show approximate body size but are subject to considerable observational errors. These are given in descriptions and key with ranges, but not treated statistically. BL was measured with the specimens whose metasoma was neither telescoped nor bent downward. Three other characters was measured with a reasonable number of specimens. The means and SD are given in Tables 1~3 and relations among them in Figs. 1~3. In the figures each polygon was drawn by connecting the outermost points of distribution and the mean was expressed by the cross point of two bars representing SD. *Tetragonula* is closely related to *Tetragonilla*. Some measurements were taken with *T. collina* Smith, the commonest species of the latter subgenus, and cited in Figs. 1~4 and 5 and Tabs. 1~15 for comparison.

Figs. 1~3 visualize considerable overlaps of many species in body size. Virtually only two species in the extremes, *T. latigenalis* and *fuscobalteata* can clearly be distinguished.

2. **Proportion:** First the lengths of about 40 body parts were measured for each species, for each sex using up to ten specimens. Then the following parts

Table 1. Mean head width (=HW, mm) in various species.

In Tables 1~15 the species are arranged in the descending order of means in worker

Species	Workers			Males		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
<i>(collina)</i>	2.437	0.031	50			
<i>latigenalis</i>	2.389	0.039	30			
<i>hirashimai</i>	2.132	0.039	30	2.040	0.044	62
<i>geissleri</i>	2.116	0.031	71	2.002	0.019	23
<i>melina</i>	2.092		3			
<i>zucchii</i>	2.040	0.031	26			
<i>sarawakensis</i>	1.912	0.038	10			
<i>laeviceps</i>	1.890	0.069	622	1.797	0.060	16
<i>gressitti</i>	1.790	0.036	53	1.775		1
<i>pagdeni</i>	1.742	0.052	483	1.677	0.038	83
<i>pagdeniformis</i>	1.729	0.046	35	1.750	0.034	120
<i>iridipennis</i>	1.693	0.060	224	1.779	0.033	37
<i>minor</i>	1.596	0.023	32			
<i>fuscobalteata</i>	1.421	0.035	187	1.415	0.028	61

Table 2. Mean wing length (=WL₂, mm) in various species

Species	Workers			Males		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
<i>(collina)</i>	1.926	0.035	50			
<i>latigenalis</i>	1.727	0.051	31			
<i>melina</i>	1.558		3			
<i>geissleri</i>	1.519	0.048	71	1.439	0.020	19
<i>zucchi</i>	1.500	0.042	36			
<i>hirashimai</i>	1.472	0.047	29	1.378	0.048	60
<i>sarawakensis</i>	1.318	0.036	10			
<i>laeviceps</i>	1.311	0.062	621	1.273	0.054	16
<i>gressitti</i>	1.288	0.053	53	1.425		2
<i>pagdeniformis</i>	1.161	0.064	44	1.243	0.034	115
<i>pagdeni</i>	1.100	0.042	504	1.104	0.026	79
<i>minor</i>	1.051	0.019	32			
<i>iridipennis</i>	1.045	0.049	249	1.164	0.031	109
<i>fuscobalteata</i>	0.939	0.042	163	0.961	0.035	59

Table 3. Mean hind tibia length (=HTL, mm) in various species

Species	Workers			Males		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
<i>(collina)</i>	2.490	0.737	50			
<i>latigenalis</i>	2.336	0.068	18			
<i>geissleri</i>	2.181	0.044	73	1.904	0.034	19
<i>melina</i>	2.150		3			
<i>hirashimai</i>	2.027	0.066	28	1.717	0.065	26
<i>zucchi</i>	1.941	0.048	32			
<i>laeviceps</i>	1.797	0.069	402	1.458	0.042	16
<i>sarawakensis</i>	1.770	0.044	10			
<i>pagdeniformis</i>	1.652	0.054	37	1.416	0.044	25
<i>gressitti</i>	1.608	0.044	19	1.750		2
<i>pagdeni</i>	1.555	0.069	228	1.469	0.038	26
<i>minor</i>	1.533	0.028	31			
<i>iridipennis</i>	1.511	0.082	180	1.547	0.049	25
<i>fuscobalteata</i>	1.321	0.047	98	1.250	0.035	25

were chosen and measured with additional specimens for comparison of various proportions: HW, WL₂, HTL (cf. above), EL (eye length), MOD and LOD (maximum and lower interorbital distances), IOD (interocellar distance), OOD (ocellocular distance), GW and EW (maximum width of gena and eye measured in profile), ML (minimum malar length), SC (length of scape seen laterally), FL and FW (length and width of flagellomere IV, both seen frontally), HTW and HBW (maximum width of hind tibia and hind basitarsus). The number of measured specimens varies by body parts even in the species represented by many available

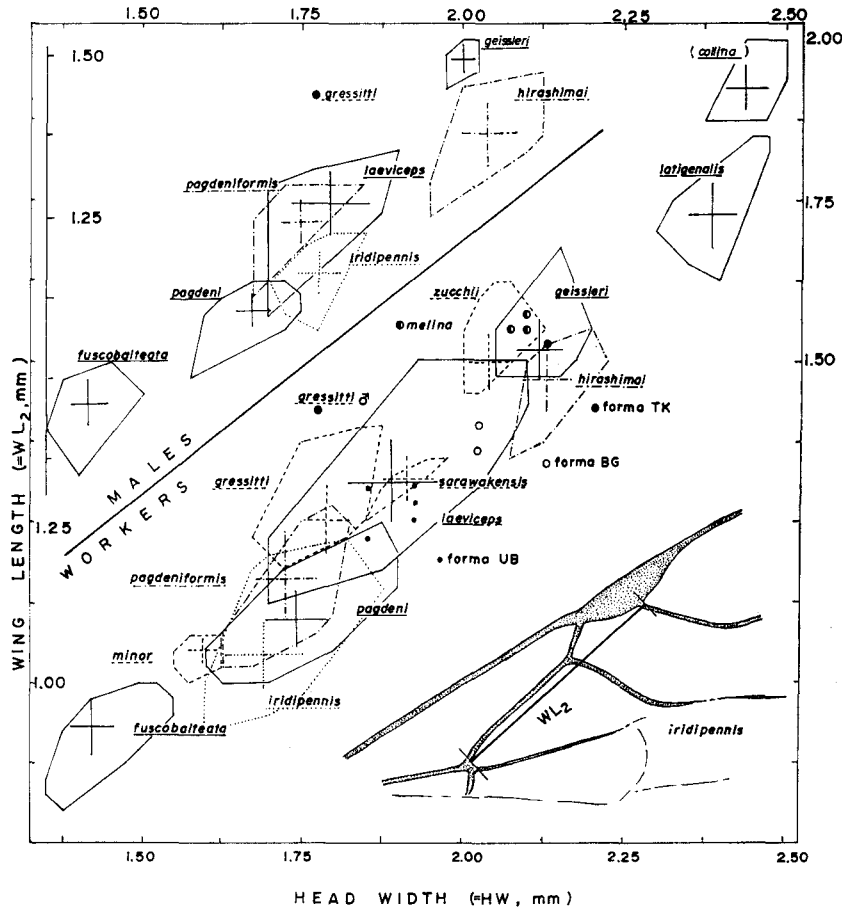


Fig. 1. Relation of wing length (WL_2) to head width (HW). Each polygon represents the outermost range of distribution of measured values. Mean is shown by the cross point of two bars representing SD.

specimens, being many for HW and WL_2 , lesser for HTL, IOD, OOD and often up to 20 for other parts. From these measurements, the following ratios were calculated (Tabs. 4-15, *workers alone): WL_2/HW , HTL/HW , HTL/WL_2 , EL/MOD , LOD/MOD , IOD/OOD^* , GW/EW^* , ML/FW^* , SC/EL , FL/FW , HTW/HTL and HBW/HTW . The observational errors of these ratios must be variable, probably higher in GW/EW where orientation of each specimen should affect the measurement and in FL/FW , ML/FW , IOD/OOD due to the small size of the parts measured.

The tables give some trends. First, some ratios vary allomorphically, the

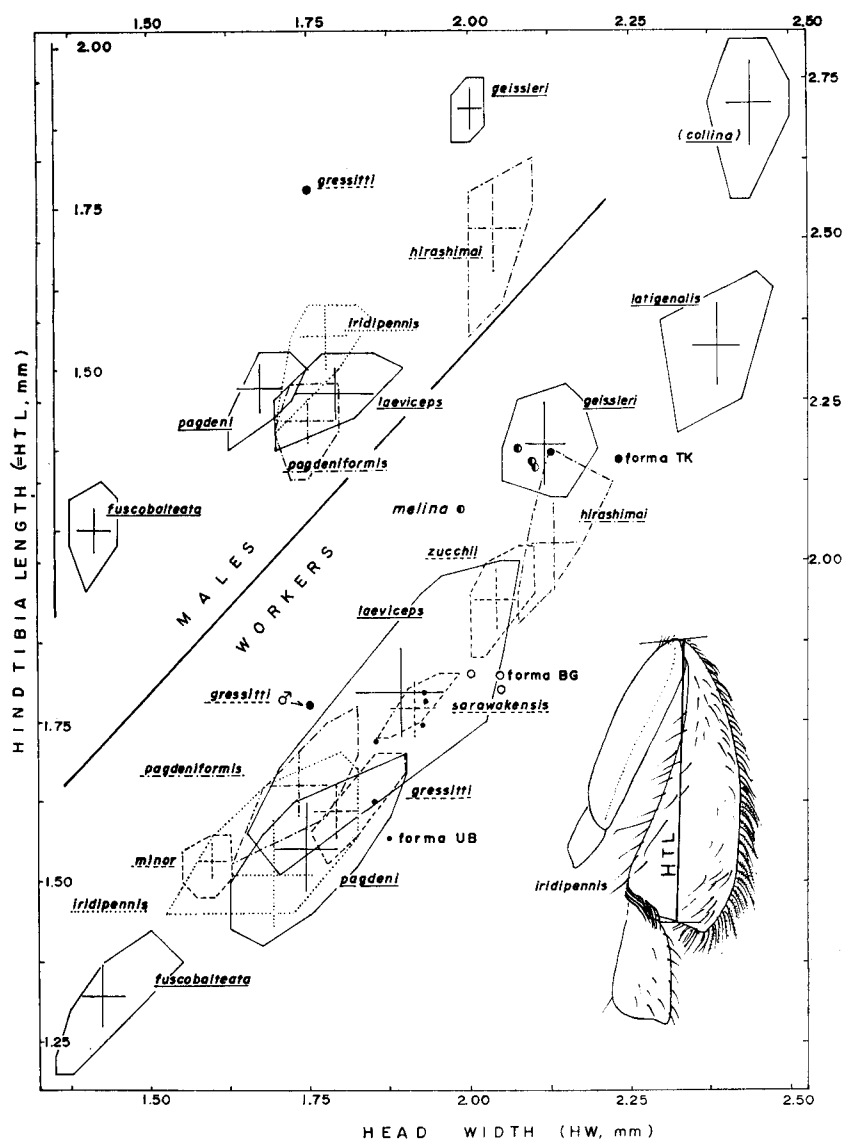


Fig. 2. Relation of hind tibia length (HTL) to head width (HW). Explanations in Fig. 1.

values becoming larger (or smaller) corresponding to the absolute body size. Fig. 4 presents some of these cases in relation to WL_2 (using reciprocal for IOD/OOD). The similar tendency is recognized in males, too, in WL_2/HW , MOD/LOD and

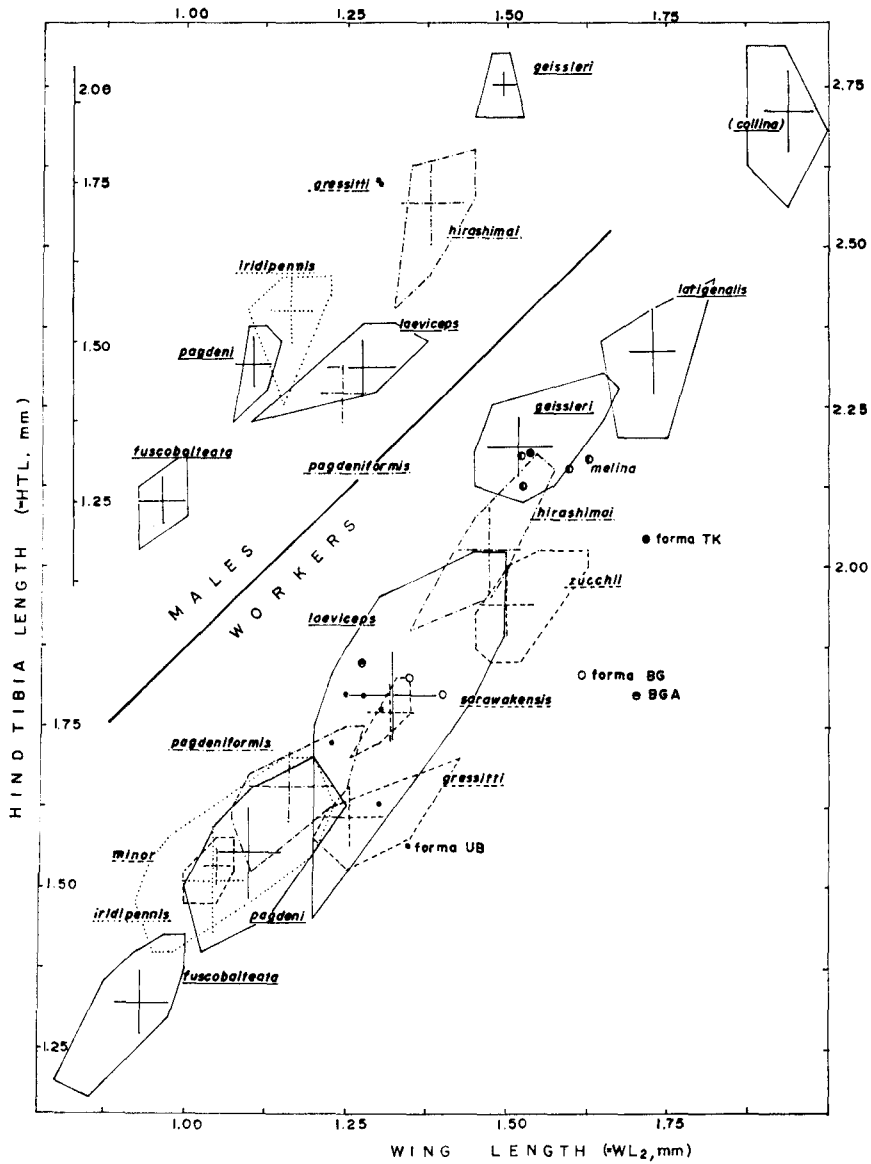


Fig. 3. Relation of hind tibia length (HTL) to wing length (WL₂). Explanations in Fig. 1.

Table 4. Ratio WL₂/HW in various species. H=Descending order of mean HW in workers

Species	Workers										Males							
	H	$\bar{x}$	N	Frequency distribution						$\bar{x}$	N	Frequency distribution						
				.60 ~	.65 ~	.70 ~	.75 ~	.80 ~	.85 ~			.60 ~	.65 ~	.70 ~	.75 ~	.80 ~	.85 ~	
<i>(collina)</i>	(0)	.82	50				2	47	1									
<i>zucchii</i>	5	.78	20				15	5										
<i>latigenalis</i>	1	.77	30			4	26											
<i>melina</i>	4	.77	3				3											
<i>geissleri</i>	3	.76	66			16	41	9		.78	21				16	5		
<i>gressitti</i>	8	.76	25			7	16	2		.87	1							1
<i>laeviceps</i>	7	.73	654		31	400	222	1		.73	17		3	8	5	1		
<i>hirashimai</i>	2	.72	23		4	17	2			.72	56		1	53	2			
<i>sarawakensis</i>	6	.72	10			10												
<i>pagdeniformis</i>	10	.72	29		3	23	3			.75	69				33	36		
<i>minor</i>	12	.72	32		4	28												
<i>fuscobalteata</i>	13	.68	185	4	134	47				.71	54	2	7	44	1			
<i>pagdeni</i>	9	.67	518	30	450	38				.70	77		29	48				
<i>iridipennis</i>	11	.66	192	64	113	15				.69	40	1	20	19				

Table 5. Ratio HTL/HW in various species. H as in Table 4

Species	Workers												Males							
	H	$\bar{x}$	N	Frequency distribution								$\bar{x}$	N	Frequency distribution						
				.85	.90	.95	1.00	1.05	1.10	1.15	1.20			.75	.80	.85	.90	.95	1.00	
				~	~	~	~	~	~	~	~			~	~	~	~	~	~	
(collina)	(0)	1.15	50						2	21	26	1								
geissleri	3	1.07	71				10	51	10			1.00	16						8	8
melina	4	1.07	3						3											
latigenalis	1	1.02	16			2	12		2											
pagdeniformis	10	1.00	39			15	24					0.85	24		10	14				
minor	12	1.00	30			14	16													
zucchii	5	0.99	22			12	10													
hirashimai	2	0.98	22		2	13	6		1			0.87	24		4	14	6			
laeviceps	7	0.98	271		20	166	85					0.85	16	3	2	10	1			
sarawakensis	6	0.97	10			10														
fuscobalteata	13	0.96	135		29	104	2					0.93	25			1	20	4		
iridipennis	11	0.94	249	19	131	94	5					0.90	28			10	17	1		
gressitti	8	0.92	17	1	15	1						1.02	1							1
pagdeni	9	0.92	342	19	239	83	1					0.92	29			3	25	1		

FL/FW. Second, some deviations from the trend lines are recognized. For instance, *T. hirashimai* possesses many body parts relatively small in relation to its absolute body size. Among five smallest species, *T. pagdeniformis* and *minor*

Table 6. Ratio HTL/WL₂ in various species. W=Descending order of mean WL₂ in workers

Species	Workers										Males						
	W	$\bar{x}$	N	Frequency distribution							$\bar{x}$	N	Frequency distribution				
				1.05	1.15	1.25	1.35	1.45	1.55	1.65			1.05	1.15	1.25	1.35	
				~	~	~	~	~	~	~			~	~	~	~	~
<i>iridipennis</i>	12	1.49	204				1	53	104	43	3	1.37	23			6	17
<i>minor</i>	11	1.49	30					2	27	1							
<i>geissleri</i>	3	1.48	67					16	49	2	1.31	18			17	1	
<i>fuscobalteata</i>	13	1.47	89					34	49	6	1.33	23			15	8	
<i>pagdeniformis</i>	9	1.46	40					18	17	5	1.17	25	6	19			
<i>pagdeni</i>	10	1.45	309				3	137	166	3	1.36	25			9	16	
(<i>collina</i>)	(0)	1.43	50					23	27								
<i>melina</i>	2	1.42	3					2	1								
<i>hirashimai</i>	5	1.42	21					16	5		1.28	23		3	19	1	
<i>laeviceps</i>	7	1.39	382	2	2	70	237	71			1.15	15	7	8			
<i>sarawakensis</i>	6	1.39	8					8									
<i>latigenalis</i>	1	1.38	15				3	11	1								
<i>zucchii</i>	4	1.32	29				22	7									
<i>gressitti</i>	8	1.27	18		8	9	1				1.37	2					2

Table 7. Ratio EL/MOD in various species. H=Descending order of mean HW in workers

Species	Workers										Males					
	H	$\bar{x}$	N	Frequency distribution					$\bar{x}$	N	Frequency distribution					
				.85	.90	.95	1.00	1.05			1.00	1.05	1.10	1.15	1.20	
				~	~	~	~	~			~	~	~	~	~	
<i>pagdeniformis</i>	10	1.03	34				3	26	5	1.19	63			3	41	19
<i>minor</i>	12	1.02	31					29	2							
<i>sarawakensis</i>	6	1.01	10				1	9								
<i>geissleri</i>	3	1.00	70				22	48	1.13	22			19	3		
<i>gressitti</i>	8	1.00	21				10	11	1.12	1			1			
<i>hirashimai</i>	2	0.99	21				10	11	1.14	63		6	33	21	3	
<i>fuscobalteata</i>	13	0.99	107				36	70	1.11	60		18	36	6		
<i>laeviceps</i>	7	0.99	211		2	128	79	2	1.17	16		3	9	4		
<i>zucchii</i>	5	0.98	28		3	11	14									
<i>melina</i>	4	0.97	3				3									
<i>pagdeni</i>	9	0.97	163		87	76			1.08	79	6	55	18			
<i>iridipennis</i>	11	0.97	177	1	88	87	1		1.08	99	16	66	17			
<i>latigenalis</i>	1	0.92	31	2	28	1										
(<i>collina</i>)	(0)	0.90	19	3	16											

behave similarly while the other three, *T. pagdeni*, *iridipennis* and *fuscobalteata* form another series as to WL₂/HW, HTL/HW and ML/FW, though *fuscobalteata*,

Table 8. Ratio LOD/MOD in various species. H as in Table 7

Species	Workers							Males						
	H	$\bar{x}$	N	Frequency distribution				$\bar{x}$	N	Frequency distribution				
				.65~	.70~	.75~	.80~			.55~	.60~	.65~	.70~	
<i>(collina)</i>	(0)	0.79	19			12	7							
<i>latigenalis</i>	1	0.79	30			18	12							
<i>melina</i>	4	0.77	3			3								
<i>zucchii</i>	5	0.77	30		2	27	1							
<i>laeviceps</i>	7	0.75	147		67	77	3	0.62	16	1	11	4		
<i>sarawakensis</i>	6	0.75	10		5	5								
<i>gressitti</i>	8	0.75	17		6	11		0.70	1				1	
<i>geissleri</i>	3	0.74	19		11	8		0.65	10		3	7		
<i>hirashimai</i>	2	0.74	14		10	4		0.66	62		8	54		
<i>pagdeni</i>	9	0.73	149		130	19		0.66	79		8	69	2	
<i>iridipennis</i>	11	0.73	111	1	94	15	1	0.68	105		1	86	18	
<i>pagdeniformis</i>	10	0.71	29	9	20			0.64	49		35	14		
<i>fuscobalteata</i>	13	0.70	93	30	62	1		0.64	60		37	23		
<i>minor</i>	12	0.69	30	18	12									

Table 9. Ratio IOD/OOD of workers in various species. H as in Table 8

Species	H	$\bar{x}$	N	Frequency distribution											
				1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1
				~	~	~	~	~	~	~	~	~	~	~	~
<i>fuscobalteata</i>	13	1.79	123								50	49	10	13	1
<i>pagdeni</i>	9	1.79	309						15	56	112	86	27	11	2
<i>iridipennis</i>	11	1.78	159						5	37	60	10	6	20	11
<i>minor</i>	12	1.71	30							13	15	2			
<i>pagdeniformis</i>	10	1.64	42					5	7	15	14	1			
<i>gressitti</i>	8	1.62	22						4	16	2				
<i>geissleri</i>	3	1.56	21					3	10	5	3				
<i>sarawakensis</i>	6	1.55	10						8	2					
<i>laeviceps</i>	7	1.54	198				7	46	79	63	3				
<i>hirashimai</i>	2	1.53	26				3	7	6	9	1				
<i>zucchii</i>	5	1.38	37			4	23	5	5						
<i>melina</i>	4	1.26	3		1	1	1								
<i>latigenalis</i>	1	1.17	19	3	6	10									
<i>(collina)</i>	(0)	1.11	20	9	10	1									

the smallest species, has some body parts relatively larger than the other two. Some species are quite characteristic by the proportion of certain body parts, e.g. *T. latigenalis* with a large GW (Fig. 4, righthand Fig. 101) and *T. gressitti* with a relatively large ML. The ratio HTW/HTL shows an interesting sexual difference (Fig. 5). In workers the ratio is typically isomorphic, but in males a conspicuous divergence among species appears, serving as a useful diagnostic character.

Table 10. Ratio GW/EW of workers in various species. H as in Table 9

Species	H	$\bar{x}$	N	Frequency distribution							
				0.5~	0.6~	0.7~	0.8~	0.9~	1.0~	1.1~	1.2~
<i>latigenalis</i>	1	1.11	19						4	13	2
<i>melina</i>	4	1.00	3						3		
<i>zucchii</i>	5	0.85	23		1	5	10	7			
<i>geissleri</i>	3	0.79	33			23	7	2	1		
<i>gressitti</i>	8	0.78	19		5	6	4	4			
<i>iridipennis</i>	11	0.78	97		16	29	49	3			
(<i>collina</i>)	(0)	0.77	20			14	6				
<i>pagdeni</i>	9	0.76	43		12	11	19	1			
<i>laeviceps</i>	7	0.74	166	2	28	101	32	3			
<i>fuscobalteata</i>	13	0.74	82		25	48	9				
<i>pagdeniformis</i>	10	0.72	21		8	10	3				
<i>minor</i>	12	0.72	10		3	6	1				
<i>sarawakensis</i>	6	0.71	12		5	6	1				
<i>hirashimai</i>	2	0.68	21		7	11	3				

Table 11. Ratio ML/FW of workers in various species. H as in Table 4

Species	H	$\bar{x}$	N	Frequency distribution				
				0.1~	0.2~	0.3~	0.4~	0.5~
(<i>collina</i>)	(0)	0.48	20				9	11
<i>latigenalis</i>	1	0.46	8				5	3
<i>gressitti</i>	8	0.36	9			9		
<i>zucchii</i>	5	0.34	29			28	1	
<i>laeviceps</i>	7	0.30	112		54	58		
<i>melina</i>	4	0.29	3		2	1		
<i>geissleri</i>	3	0.28	30		18	12		
<i>sarawakensis</i>	6	0.28	10		5	5		
<i>hirashimai</i>	2	0.26	14	1	10	3		
<i>fuscobalteata</i>	13	0.25	50	1	49			
<i>pagdeni</i>	9	0.24	50		49	1		
<i>iridipennis</i>	11	0.22	33	1	32			
<i>pagdeniformis</i>	10	0.20	34	12	22			
<i>minor</i>	12	0.16	29	25	4			

Another aspect worth mentioning is a remarkable sexual difference of HTL in some species (cf. also Figs. 2, 3).

Figs. 6 and 7 give the percentage deviations from the interspecific means (of 13 species in workers and 8 species in males) of various characters for each species. Similar variation trends are recognized in three groups: 1) *pagdeni-iridipennis-fuscobalteata* (both sexes), 2) *pagdeniformis-minor* (workers) and 3) *hirashimai-laeviceps-sarawakensis* (workers). The figures also show smaller variations in LOD/MOD and MOD/EL in both sexes and HTW/HTL and HBW/HTW in workers.

Table 12. Ratio SC/EL in various species. H as in Table 4

Species	Workers						Males					
	H	$\bar{x}$	N	Frequency distribution				$\bar{x}$	N	Frequency distribution		
				.45~	.50~	.55~	.60~			.35~	.40~	.45~
(collina)	(0)	0.60	20			6	14					
gressitti	8	0.59	9			7	2	0.46	1			1
zucchii	5	0.56	20		8	12						
hirashimai	2	0.55	9		2	7		0.44	13		8	5
melina	4	0.55	3		1	2						
geissleri	3	0.55	20		8	12		0.44	20		17	3
pagdeni	9	0.55	20		10	10		0.43	17	1	12	4
latigenalis	1	0.55	15		10	5						
laeviceps	7	0.54	20		11	9		0.40	13	6	7	
iridipennis	11	0.53	20		18	2		0.43	20		20	
sarawakensis	6	0.53	10		10							
fuscobalteata	13	0.52	20		1	19		0.44	20		18	2
pagdeniformis	10	0.51	20	3	17			0.40	20	5	15	
minor	12	0.50	20	5	15							

Table 13. Ratio FL/FW in various species. H as in Table 4

Species	Workers									Males									
	H	$\bar{x}$	N	Frequency distribution						$\bar{x}$	N	Frequency distribution							
				.6 ~	.7 ~	.8 ~	.9 ~	1.0 ~	1.1 ~			1.0 ~	1.1 ~	1.2 ~	1.3 ~	1.4 ~	1.5 ~	1.6 ~	
<i>geissleri</i>	3	1.06	30						29	1	1.48	17					14	2	1
<i>(collina)</i>	(0)	1.02	20				1	19											
<i>latigenalis</i>	1	0.98	8					4	4										
<i>hirashimai</i>	2	0.97	21				14	7		1.19	20		11	9					
<i>zucchii</i>	5	0.94	30			3	22	5											
<i>melina</i>	4	0.93	3				3												
<i>laeviceps</i>	7	0.92	129			36	92	1		1.15	14	3	8	3					
<i>sarawakensis</i>	6	0.91	10			3	7												
<i>fuscobalteata</i>	13	0.90	29			10	19			1.05	20	18	1		1				
<i>gressitti</i>	8	0.86	9		1	4	4			1.27	1			1					
<i>pagdeniformis</i>	10	0.82	34		12	20	2			1.13	23	9	10	4					
<i>pagdeni</i>	9	0.81	50		22	26	2			1.07	20	16	4						
<i>iridipennis</i>	11	0.81	33		12	21				1.09	20	14	6						
<i>minor</i>	12	0.78	30	2	20	8													

Finally two conspicuous deviations from general trends are mentioned: 1) Workers of *T. latigenalis* have a very wide ocelloccipital distance, nearly as wide as ocellar diameter (Fig. 103) whereas in other species ocelloccipital distance is about as long as 1/2 ocellar diameter (Fig. 104). 2) Males of *T. geissleri* have fairly wide metasoma, ratio HW/ maximum metasomal width being 0.75~0.80, whereas more

Table 14. Ratio HTW/HTL in various species. T=Descending order of mean HTL in workers

Species	Workers										Males												
	T	$\bar{x}$	N	Frequency distribution								$\bar{x}$	N	Frequency distribution									
				.30	.32	.34	.36	.38	.40	.42	.26			.28	.30	.32	.34	.36	.38	.40	.42		
				~	~	~	~	~	~	~	~			~	~	~	~	~	~	~	~		
<i>(collina)</i>	(0)	0.37	19					12	7														
<i>pagdeni</i>	10	0.37	350			25	30	123	130	38	4	0.40	25					1	5	12	7		
<i>sarawakensis</i>	7	0.37	10					8	2														
<i>zucchii</i>	5	0.36	32				7	20	5														
<i>iridipennis</i>	12	0.36	121			24	16	55	26		0.38	25				2	5	13	5				
<i>latigenalis</i>	1	0.35	8				2	6															
<i>geissleri</i>	2	0.35	71			3	47	21			0.34	18				7	10	1					
<i>hirashimai</i>	4	0.35	25			1	18	4	2		0.30	25	2	4	16	3							
<i>melina</i>	3	0.35	3				3																
<i>laeviceps</i>	6	0.35	348			26	157	154	11		0.33	14			2	6	6						
<i>gressitti</i>	9	0.34	15	1	3	10	1				0.28	2	1	1									
<i>pagdeniformis</i>	8	0.34	43	1	13	24	3	2			0.29	23		12	10	1							
<i>minor</i>	11	0.34	31			9	20	2															
<i>fuscobalteata</i>	13	0.34	135	1	38	76	18	2			0.36	25			3	9	8	5					

Table 15. Ratio HBW/HTW in various species. T as in Table 14

Species	Workers								Males									
	T	$\bar{x}$	N	Frequency distribution					$\bar{x}$	N	Frequency distribution							
				.45	.50	.55	.60	.65			.30	.35	.40	.45	.50	.55	.60	.65
				~	~	~	~	~			~	~	~	~	~	~	~	~
<i>gressitti</i>	9	0.61	16		1	6	7	2	0.54	2					1	1		
<i>geissleri</i>	2	0.58	16		4	5	6	1	0.53	10				1	6	3		
<i>hirashimai</i>	4	0.58	19		1	12	6		0.56	18					7	6	5	
<i>latigenalis</i>	1	0.58	18		4	8	6											
<i>zucchii</i>	5	0.58	24		2	16	6											
<i>laeviceps</i>	6	0.57	65		3	32	30		0.55	16					4	12		
<i>sarawakensis</i>	7	0.56	10		3	6	1											
<i>pagdeniformis</i>	8	0.56	35		14	15	6		0.61	25					1	10	12	2
<i>(collina)</i>	(0)	0.54	20		14	6												
<i>iridipennis</i>	12	0.53	95	8	65	20	2		0.49	22			2	8	12			
<i>minor</i>	11	0.53	10	1	5	4												
<i>melina</i>	3	0.52	3	1	2													
<i>pagdeni</i>	10	0.52	53	10	38	5			0.43	26		2	18	6				
<i>fuscobalteata</i>	13	0.51	50	12	31	7			0.44	24	1	7	14	1	1			

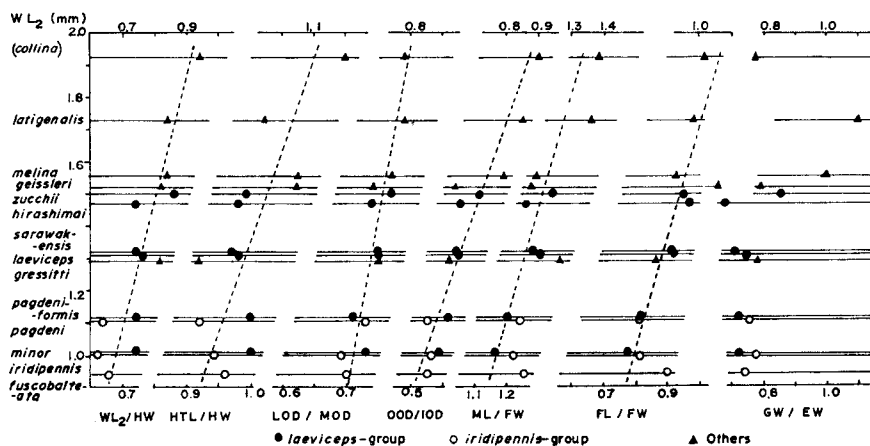


Fig. 4. Relation of various ratios among body parts to absolute body size (represented by WL_2) in workers. Species groups are defined in p. 234. Trend lines given by eye.

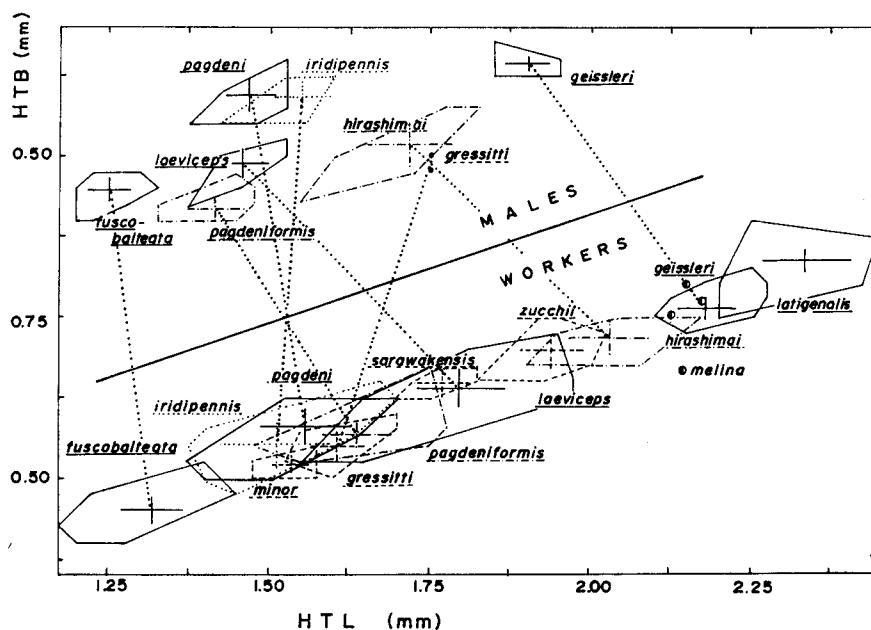


Fig. 5. Ratio HTW/HTL in males and workers. Further explanations in Fig. 1.

Table 16. Specific difference in color variation of clypeus. In bicolourous specimens, the paler part was chosen. In Tables 16~22 the species are arranged from darker to paler ones (in workers). Males of *T. geissleri* were excluded as most were callows.

Species	Workers					Males			
	N	III	IV	V	VI	N	IV	V	VI
<i>iridipennis</i>	194		8	56	130	79		11	68
<i>gressitti</i>	50		2	24	24				
<i>minor</i>	32		3	21	8				
<i>pagdeniformis</i>	49	1	7	28	13	120	6	110	4
<i>hirashimai</i>	26		11	14	1	51		51	
<i>zucchii</i>	37		17	17	3				
<i>fuscobalteata</i>	131	19	55	55	2	57	5	45	7
<i>geissleri</i>	67	3	32	30	2				
<i>laeviceps</i>	483	37	216	206	24	13	1	11	1
<i>pagdeni</i>	441	19	215	197	10	79	4	52	23
<i>latigenalis</i>	19	14	5						
<i>sarawakensis</i>	10	10							

Table 17. Specific difference in color variation of tegula.

Species	Workers					Males				
	N	III	IV	V	VI	N	III	IV	V	VI
<i>gressitti</i>	55				55	1				1
<i>latigenalis</i>	31			27	4					
<i>iridipennis</i>	287	7	38	179	63	110		37	69	4
<i>pagdeniformis</i>	49		6	40	3	119	2	9	107	1
<i>laeviceps</i>	681	104	242	322	13	13		3	8	2
<i>minor</i>	32		16	16						
<i>geissleri</i>	64	1	29	27	7					
<i>fuscobalteata</i>	152	17	70	63	2	58		27	31	
<i>pagdeni</i>	494	109	301	84		82	2	74	5	1
<i>hirashimai</i>	35	7	21	7		62		22	40	
<i>zucchii</i>	31	8	23							
<i>sarawakensis</i>	10	10								

than 1.0 and usually more than 1.1 in all other species and workers of *T. geissleri*.

3. **Coloration:** In all examined species wings are transparent with no or few infuscation. Except *T. melina*, which possesses uniformly honey yellow coloration, all other species recorded in the present paper are basically black. The tone is darkest on mesosomal dorsum and face above, often becoming paler on other body parts. In workers the palest parts are scape and flagella below, which are usually testaceous to fulvous in all species except *T. gressitti*, whereas these parts are often darker in males (Tab. 21). Other parts frequently becoming paler are

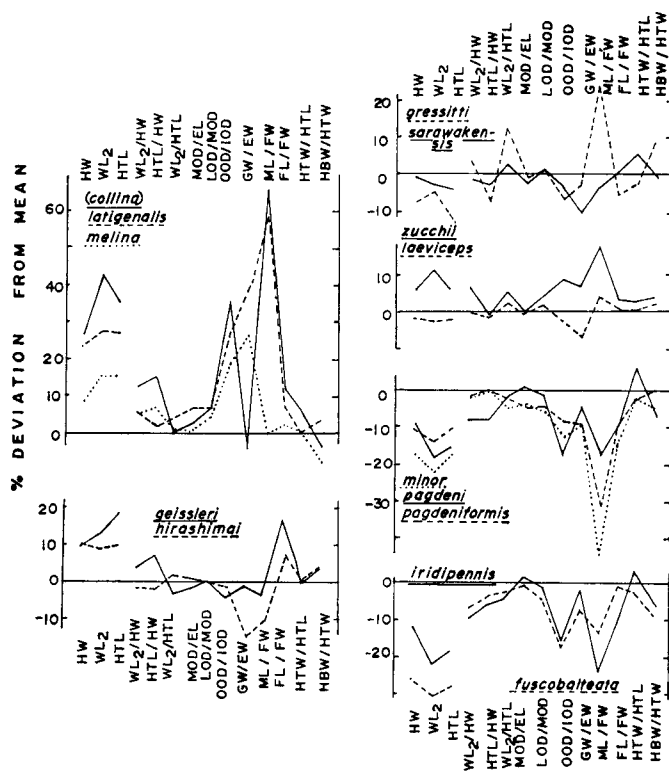


Fig. 6. Percentage deviations from interspecific means of various characters in each species (workers). NB: WL_2/HTL , MOD/EL and OOD/IOD are shown by reciprocals of the values given in Tabs. 6, 7, 9.

clypeus, tegula, basal metasomal terga and some parts of legs, particularly trochanters and tarsi. But coloration varies considerably within the same species, so that the following body parts were examined with many specimens: Clypeus, tegula, fore trochanter, hind tibia and metasomal dorsum. Color hue was arbitrarily divided in six degrees: I. pale fulvous, II. fulvous, III. pale testaceous or ferruginous, IV. chestnut or dark brown, V. blackish brown, VI. brownish black to black. Apparently this distinction is not free from subjective judgement, but some tendencies are recognized from Tabs. 16~20. *T. gressitti* is most melanic and *T. sarawakensis* is palest. *T. latigenalis* is in general melanic but clypeus is relatively pale. Two allied species, *T. pagdeni* and *T. iridipennis* are distinct in most body parts, the former being paler. Concerning metasoma, *T. pagdeni* is much paler than suggested in Table 20, because this species frequently shows the bicolourous metasoma.

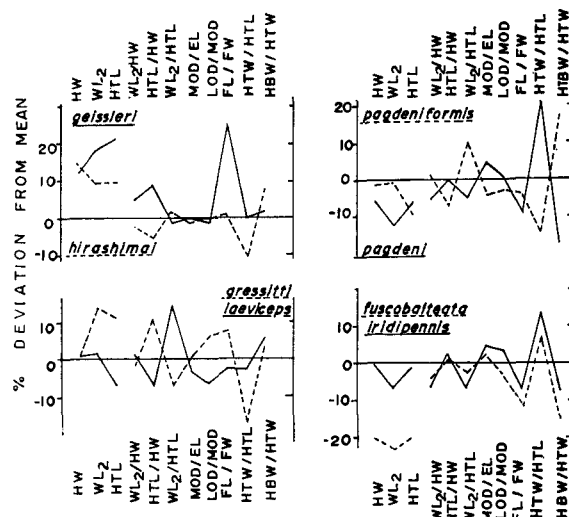


Fig. 7. Percentage deviations from interspecific means of various characters in each species (males).

Table 18. Specific difference in color variation of fore trochanter

Species	Workers					Males				
	N	II	III	IV	V	N	II	III	IV	V
<i>gressitti</i>	55				55	2				2
<i>latigenalis</i>	31		1	29	1					
<i>iridipennis</i>	264	2	90	146	26	108			63	45
<i>minor</i>	26		4	21	1					
<i>pagdeniformis</i>	52	3	18	31		96		57	37	2
<i>geissleri</i>	67		56	11						
<i>laeviceps</i>	644	16	514	114		13		9	4	
<i>hirashimai</i>	32		30	2		62		61	1	
<i>zucchii</i>	39	6	28	5						
<i>fuscobalteata</i>	180	19	145	16		56		11	38	7
<i>pagdeni</i>	577	45	477	55		92	1	16	65	10
<i>sarawakensis</i>	10	6	4							

Nevertheless, color variation is considerable for most body parts studied. Only *T. melina*, *gressitti* and *sarawakensis* can be safely sorted by coloration. Descriptions of new forms with a few specimens on the basis of coloration of tegula, stigma, etc. as practiced previously, are virtually meaningless.

A peculiar feature of stingless bees which may relate with ample color variation is mentioned. Stingless bee workers are on the average much long lived than honeybee workers.

Table 19. Specific difference in color variation of hind tibia. In bicolorous specimens the darker part was chosen

Species	Workers						Males				
	N	II	III	IV	V	VI	N	III	IV	V	VI
<i>gressitti</i>	54					54	2		1	1	
<i>iridipennis</i>	269		2	11	95	161	109		39	63	7
<i>minor</i>	32				12	20					
<i>geissleri</i>	69			25	32	17					
<i>latigenalis</i>	31			3	20	8					
<i>fuscobalteata</i>	200	8	21	53	89	29	60		27	29	4
<i>pagdeniformis</i>	53			11	38	4	119	4	57	57	1
<i>zucchii</i>	39		2	15	18	4					
<i>laeviceps</i>	692	2	47	214	294	135	13		6	6	1
<i>pagdeni</i>	577		23	257	270	27	82	2	70	10	
<i>hirashimai</i>	34			21	12	1	62	5	46	11	
<i>sarawakensis</i>	10		6	4							

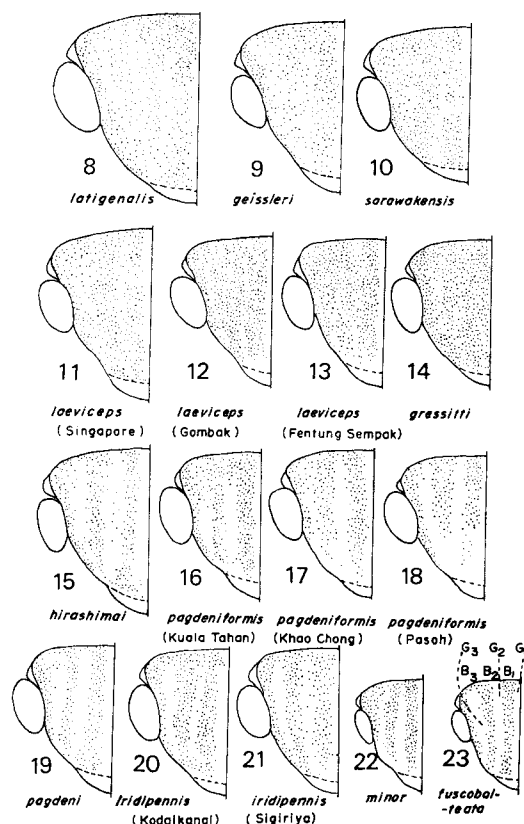
Table 20. Specific difference in color variation of metasomal dorsum. In bicolorous specimens, the darker part was chosen.

Species	Workers						Males				
	N	II	III	IV	V	VI	N	III	IV	V	VI
<i>gressitti</i>	55				6	49	2				2
<i>latigenalis</i>	31				3	28					
<i>pagdeniformis</i>	51			4	23	24	117		7	72	38
<i>hirashimai</i>	31			2	19	10	52	1	23	25	3
<i>geissleri</i>	68			12	41	15					
<i>minor</i>	32			3	19	10					
<i>laeviceps</i>	690		9	143	336	202	13	5	7	1	
<i>iridipennis</i>	288	3	22	86	108	69	103		73	24	6
<i>pagdeni</i>	542	4	35	217	212	74	80		15	22	43
<i>fuscobalteata</i>	199	1	23	95	65	15	65	1	33	22	9
<i>zucchii</i>	37		2	15	12	8					
<i>sarawakensis</i>	10	2	8								

Their flight activity starts much later. During the house-bee period, pigmentation proceeds very slowly. Newly emerged workers are nearly whitish. Then, pigmentation goes with a definite mode, e.g. in most species mesoscutellum is pigmented much later than mesoscutum. Foraging is performed by fully pigmented old workers, only which have been usually collected and described by taxonomists. But functional and pigmental developments may not always go in parallel so that some relatively pale workers are occasionally collected on flowers, which must increase the amplitude of color variation. For variation analysis of dark colored species it is advisable to use only the specimens whose mesosomal dorsum is fully pigmented.

Table 21. Specific difference in color variation of male scape and flagella.
IV' and V' are respectively grayish or smoky black
with different brownish hue

Species	Scape					Flagella				
	N	II	III	IV'	V'	N	II	III	IV'	V'
<i>iridipennis</i>	108		2	46	60	93	5	88		
<i>fuscobalteata</i>	62		3	17	42	59		11	44	4
<i>pagdeniformis</i>	107	7	43	50	7	110		12	41	57
<i>pagdeni</i>	81	12	47	22		80	12	47	21	
<i>laeviceps</i>	13		11	2		13			2	11
<i>geissleri</i>	20		20			20		13	7	
<i>hirashimai</i>	62	10	51	1		61	42	16	3	
<i>gressitti</i>	1	1				1		1		



Figs. 8-23. Hair arrangement on worker mesoscutum. Body size conveniently divided in three classes.

4. **Pilosity:** Schwarz (1939) used hair arrangement on mesoscutum to separate *T. pagdeni* and *T. laeviceps* (=his *iridipennis*). Hairs are rather uniform in the latter while banded in the former. Unfortunately, this character cannot be used with precision. Occasionally some specimens show intermediate conditions. Further, hair arrangement is easily obscured in the specimens of poor conditions clogged with other materials, which is very common in stingless bee workers. Nevertheless, this is one of the few reliable diagnostic characters for workers. In typically banded specimens, there are six hair bands separated by five glabrous spaces ($B_1 \sim B_3$ and $G_1 \sim G_3$ in Fig. 23). B_3 and G_1 are more or less detectable in all species while B_1 , B_2 , G_2 and G_3 are distinct in some species but less or not in others (Figs. 8~23). Arranged in the descending order of HW, bands are more conspicuous in smaller species as follows (exception: *T. hirashimai*):

Not well banded	Well banded
<i>latigenalis</i>	
	<i>hirashimai</i>
<i>geissleri</i>	
<i>melina</i>	
<i>zucchii</i>	
<i>sarawakensis</i>	
<i>laeviceps</i>	
<i>gressitti</i>	
	<i>pagdeni</i>
	<i>pagdeniformis</i>
	<i>iridipennis</i>
	<i>minor</i>
	<i>fuscobalteata</i>

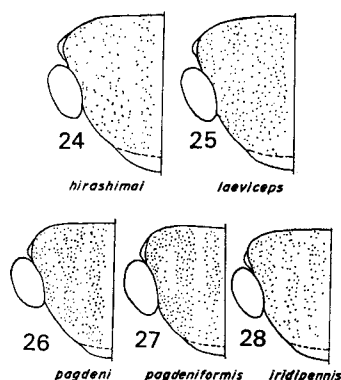
In males mesoscutal pilosity is generally sparser and bands are less conspicuous (Figs. 24~28). Instead, the hairs are generally longer, sparsely mixed with some longer hairs. The lengths of these hairs are sometimes species specific (in μ):

	long hairs	short hairs
<i>gressitti</i>	175	100
<i>hirashimai</i>	(125)~150~(175)	75~100
<i>iridipennis</i>	120~125	75~100
<i>pagdeni</i>	100~(125)	50~(75)
<i>fuscobalteata</i>	100~(125)	± 50
<i>geissleri</i>	100	± 50
<i>pagdeniformis</i>	75~100	± 50
<i>laeviceps</i>	± 75	± 50

Another, less stable character is the pilosity of the face above. Hairs are either whitish and distinctly plumose or darker and less plumose. This character is variable within the same species. Yet the tendency is clear, being somewhat parallel with band formation on mesoscutum (Table 22).

Coloration of hairs of some body parts is sometimes species-specific, though with a considerable variation. Tables 23~25 present color variations of hairs of

mesoscutal dorsum, mesoscutellar fringe (of bristles, not of pale soft hairs) and anterior corbicular bristles by using six degrees (cf. p. 180) and choosing the darker degree when the hue was variable in the same individual. The species tending to show mesoscutal bands seem to possess paler hairs. Pilosity of males legs is described below.



Figs. 24-28. Hair arrangement on male mesoscutum.

Table 22. Specific difference in plumosity of frontal hairs. +=distinctly plumose, ±=intermediate, -=not plumose

Species	Workers				Males			
	N	+	±	-	N	+	±	-
<i>geissleri</i>	55			55	12			12
<i>gressitti</i>	20			20	1			1
<i>latigenalis</i>	12			12				
<i>sarawakensis</i>	10			10				
<i>laeviceps</i>	245		13	232	18			18
<i>zucchii</i>	28		8	20				
<i>pagdeniformis</i>	34		3	31	116			116
<i>minor</i>	29			29				
<i>hirashimai</i>	21	1	20		55	2	28	25
<i>iridipennis</i>	265	132	105	28	91		6	85
<i>fuscoobalteata</i>	104	65	38	1	51	26	23	2
<i>pagdeni</i>	150	105	45		66	23	41	2

5. **Structures:** Except for thick gena and occiput in *T. latigenalis* reliable structural characters are absent in workers. All following characters concern the males.

1) *Facial contour:* *T. gressitti* (Fig. 29) has a relatively round head and eyes distinctly narrowed below. In other species head is more transverse and eyes

Table 23. Specific difference in color variation of worker mesoscutal hairs.

In Tables 23~25, the species are arranged
from darker to paler ones

Species	N	II	III	IV	V	VI
<i>latigenalis</i>	17					17
<i>gressitti</i>	55				36	19
<i>geissleri</i>	69		3	21	43	2
<i>zucchii</i>	31			5	23	3
<i>minor</i>	32		6	10	16	
<i>laeviceps</i>	386	121	167	45	53	
<i>pagdeniformis</i>	46	20	19	6	1	
<i>sarawakensis</i>	10	3	7			
<i>iridipennis</i>	176	74	37	40	19	6
<i>pagdeni</i>	240	193	39	4	4	
<i>hirashimai</i>	26	18	6	2		
<i>fuscobalteata</i>	134	115	19			

Table 24. Specific difference in color variation of darker mesoscutellar bristles

Species	Workers							Males						
	N	I	II	III	IV	V	VI	N	I	II	III	IV	V	
<i>latigenalis</i>	8					1	7							
<i>gressitti</i>	55					37	18	2			2			
<i>geissleri</i>	65			4	20	40	1	12			6	5	1	
<i>zucchii</i>	32				2	24	6							
<i>pagdeniformis</i>	49		5	8	10	26		120		4	18	64	4	
<i>laeviceps</i>	467		34	155	142	131	5	13		1	9	3		
<i>minor</i>	32		13	16	3									
<i>hirashimai</i>	27	2	8	9	6	2		62	19	41	2			
<i>sarawakensis</i>	10		8	2										
<i>pagdeni</i>	517	38	319	121	35	4		81		46	29	6		
<i>iridipennis</i>	262	15	166	27	45	9		110		11	57	34	8	
<i>fuscobalteata</i>	192	6	169	16	1			62		44	18			

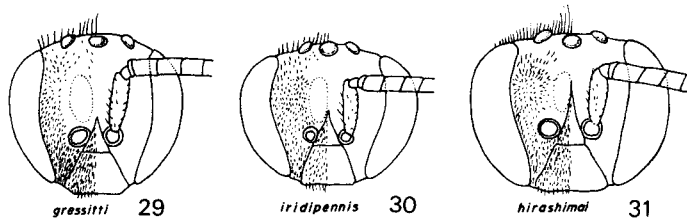
wider below. Vertex is medially slightly raised in *T. pagdeni*, *iridipennis* and *fuscobalteata* (Fig. 30) but flatter in other species (Fig. 31).

2) *Mandible*: *T. gressitti* is outstanding by the possession of mandible receded by weak development of outer tooth (Fig. 107). In other species mandible is normal, i.e. inner tooth smaller (Fig. 108).

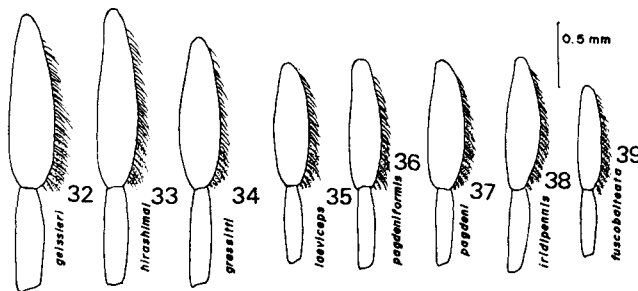
3) *Mid tibia and basitarsus* (Fig. 32~39): Admixture of plumose hairs in posterior fringe of mid tibia is particularly rich in *T. iridipennis*, *pagdeni* and *fuscobalteata*. Mid basitarsus is relatively long in *T. gressitti*, ratio to mid tibia length is 0.67 while 0.55~0.64 in other species. Posterior margin of basitarsus is imperceptibly angulate in *T. iridipennis* and *pagdeni*. But some of these differences are so subtle that are not given in descriptions.

Table 25. Specific difference in color variation of anterior hind tibial fringe

Species	Workers							Males						
	N	I	II	III	IV	V	VI	N	I	II	III	IV	V	
<i>gressitti</i>	55					34	21	2			2			
<i>geissleri</i>	64			3	22	27	12	12			1	7	4	
<i>zucchii</i>	45			1		32	12							
<i>laeviceps</i>	523			14	111	256	142	13		1	6	6		
<i>latigenalis</i>	31					23	8							
<i>hirashimai</i>	30			4	6	17	3	62	33	29				
<i>sarawakensis</i>	10				1	9								
<i>pagdeniformis</i>	48			2	10	30	6	101		20	31	65	3	
<i>minor</i>	32			7	9	16								
<i>iridipennis</i>	270	2	98	90	17	47	16	111				26	85	
<i>pagdeni</i>	522	18	282	165	51	6		82		41	30	11		
<i>fuscobalteata</i>	134		115	19				61		60	1			



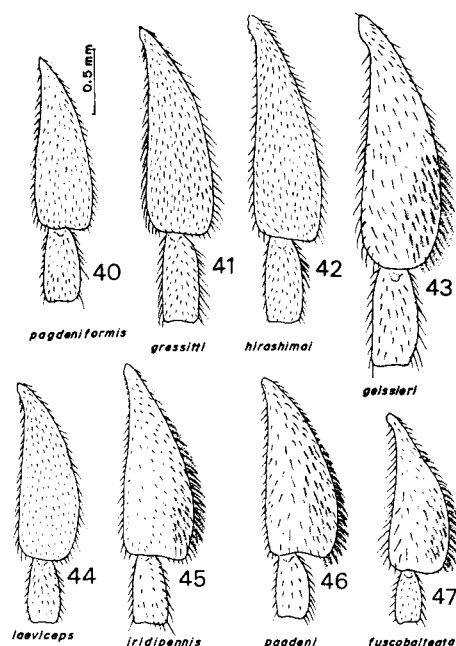
Figs. 29-31. Male head of three species viewed frontally.



Figs. 32-39. Male mid tibia and basitarsus.

4) *Hind tibia and basitarsus* (Figs. 40~61): Partly related with the specific difference in ratio HTW/HTL (Fig. 5, Tab. 14), there are two types of hind tibia:

	I	II
1. Outer surface	Homogenously flat	Medially gently convex and apically slightly depressed
2. Hairs on outer surface	Homogenously dense and short	Sparser, especially anteroapically, some ones relatively long
3. Plumose hairs	Absent	Present on outer surface posteriorly as well as in hind fringe
Species	<i>hirashimai</i> <i>gressitti</i> <i>pagdeniformis</i> <i>laeviceps</i>	<i>iridipennis</i> <i>pagdeni</i> <i>fuscobalteata</i>



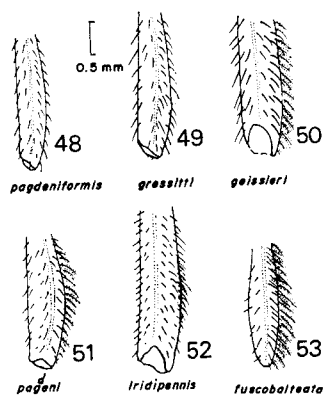
Figs. 40-47. Male hind tibia and basitarsus.

T. geissleri is intermediate. Plumose hairs are present but surface is rather flat and hairs relatively dense and short. Maximum length of hairs of hind margins of tibia and basitarsus are (in μ):

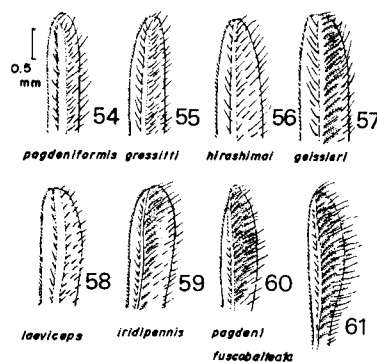
	Tibia	Basitarsus
<i>pagdeniformis</i>	75	± 75
<i>laeviceps</i>	75	$\pm 75 \sim (100)$
<i>hirashimai</i>	100	100~125
<i>iridipennis</i>	100	100
<i>pagdeni</i>	175	125
<i>fuscobalteata</i>	150	100
<i>geissleri</i>	150	125
<i>gressitti</i>	150	150

A subtle difference in the shape of hind basitarsus is noted: In *T. iridipennis* and *pagdeni* slightly divergent toward the apex but in other species subparallel.

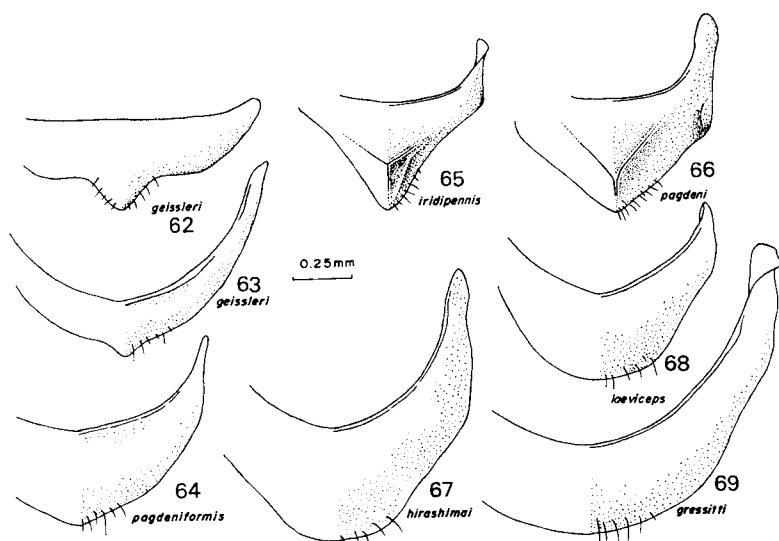
5) *Apical tergum* (Figs. 62~69): This character, used by Schwarz (1939) to distinguish *T. fuscobalteata* and *T. laeviceps* (=his *iridipennis* in S.E. Asia), is useful. *T. fuscobalteata*, *pagdeni* and *iridipennis* (redefined in the present paper) have Y-shaped edge on the tergum, the lateral sides of which are steeply inclined.



Figs. 48-53. Pilosity of apical part of male hind tibia, seen frontally.



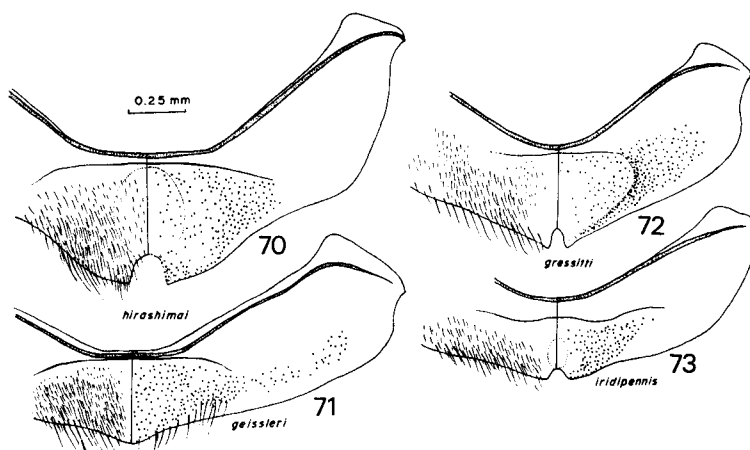
Figs. 54-61. Pilosity of apical part of male hind tibia, seen posteriorly.



Figs. 62-69. Male apical tergum. Fig. 62 in pressed condition, others in natural disposition.

No other species possess such edge. The posterior margin is medially more pointed and laterally more angulate in *T. iridipennis* than in *T. pagdeni* and *fuscobalteata*. In other species the contour of posterior margin is slightly variable, medially slightly (*T. pagdeniformis*) to distinctly pointed (*T. geissleri*) or rounded (other species).

6) *Apical metasomal sterna*: In stingless bees male metasomal sternum VIII, which is a useful character in many bees, is reduced (Michener 1944), but sterna V~VII are diagnostic of species or supra-specific taxa. Sternum V (Figs. 70~73) of five small species, *T. iridipennis*, *pagdeni*, *fuscobalteata*, *laeviceps* and *pagdeniformis* are similar: Pregladular area is medially relatively long and postgladular area is medially narrowly depressed, with small medioapical emargination. In *T. gressitti*, *hirashimai* and *geissleri*, pregladular area is medially obsolete. *T. hirashimai* has broad median depression of postgladular area with sparse and fine spots issuing short hairs and medioapical emargination relatively large. *T. gressitti* has median area very widely free from coarse spots and stout hairs, and medioapical emargination narrow. *T. geissleri* has median area less differentiated and medioapical area transparent but not emarginate.

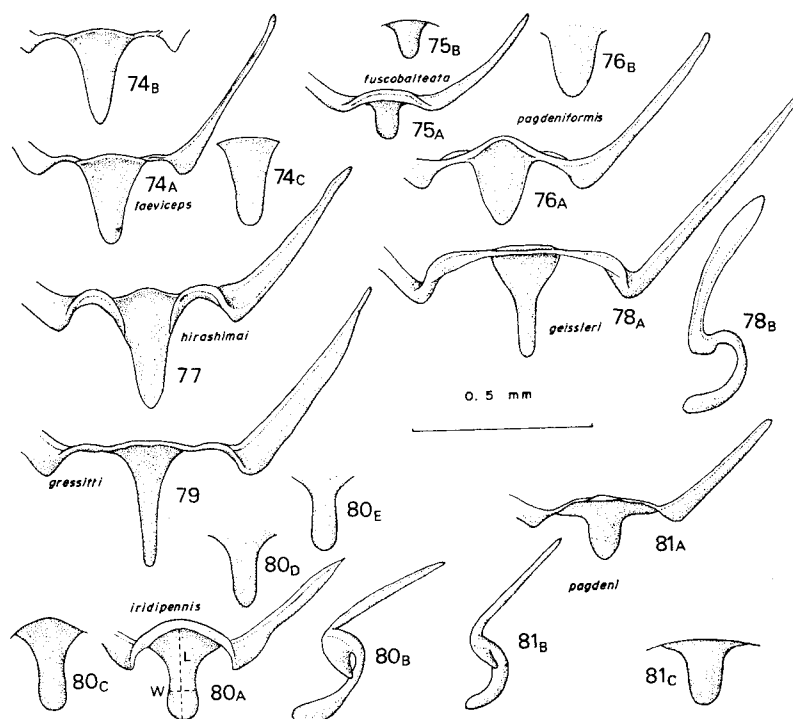


Figs. 70-73. Male sternum V (S_5) in four species.

Sternum VI (Figs. 74~81) is species specific in the curvature of antecosta medially and the shape of medioapical process. Antecostal curvature is distinct in *T. iridipennis*, *pagdeniformis* and to some degree also in *pagdeni* and *fuscobalteata* while milder in other larger species. Medioapical process is short and relatively wide in smaller species while longer in others, especially in *T. gressitti*. Length/width is given by *distance between apex of process to apical margin of antecosta/width of process at the point about 1/3 length from apex* (cf. Fig. 80A).

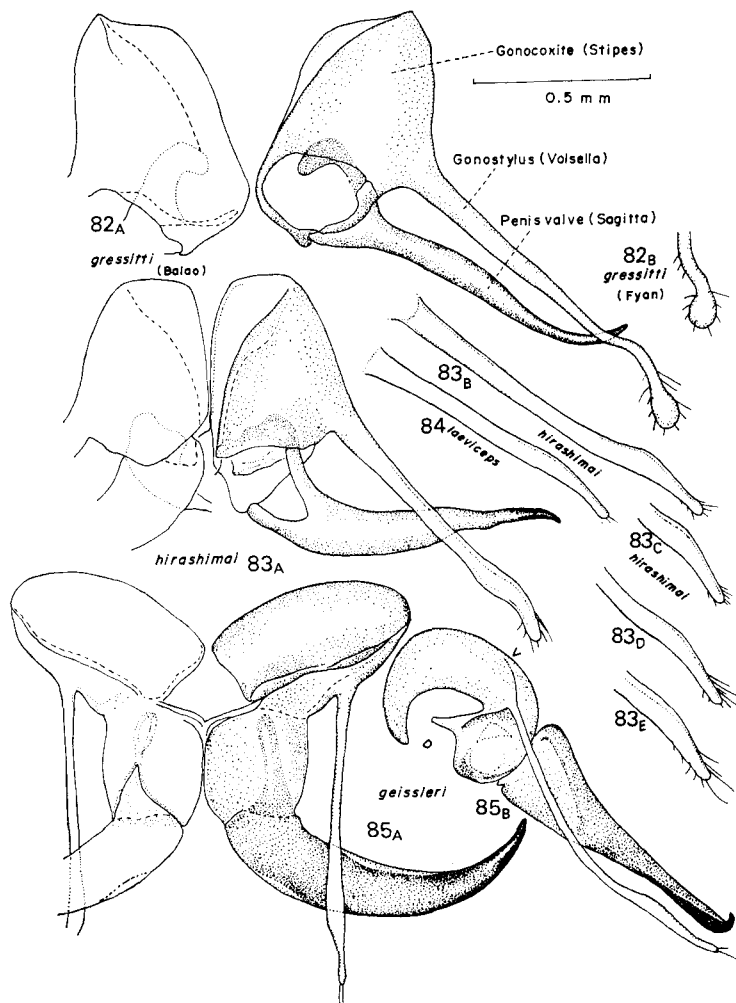
Sternum VII is triangular in all species examined. Ratio length/width and

curvature of lateral margin seem species-specific. But these features vary among individuals and the number of studied specimens is not large enough so that these are not given in descriptions (Figs. 111~117).



Figs. 74-81. Male sternum VI (S_6). Figures for the same species are shown by the same numeral with alphabetic suffices. Figs. 78B, 80B and 81B=lateral view, others=dorsal view.

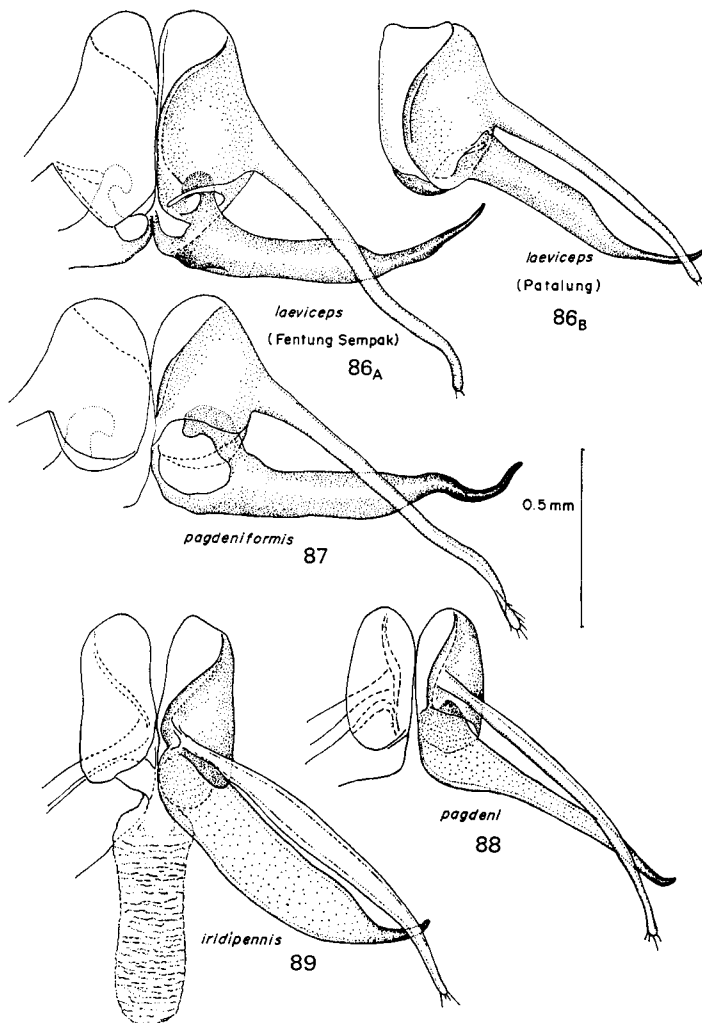
7) *Genitalia* (Figs. 82~100): Male genitalia are the best diagnostic character complex. But the shape of various parts can be seen quite differently according to the orientation of materials. Whether both gonocoxites lie in parallel or divergently gives a fairly different appearance (compare Figs. 83A, 86A~89 with 82A and 85A). By this reason the contour of gonocoxite and structure of junction between gonocoxite and penis valve are not used for description, despite the presence of some specific differences are suggested. Most reliable characters are shape of gonostylus and penis valve. In general gonostylus is long and slender, more or less sinuous with sparse hairs at apex, penis valve is very robust, tapering only at the apex, about as long as or slightly shorter than gonostylus. Three species, *T. iridipennis*, *pagdeni* and *fuscobalteata* differ from others by gonostylus arising from the dorsum of gonocoxite.



Figs. 82-85. Male genitalia of *T. gressitti*, *hirashimai* and *geissleri*. The same species is shown by the same numeral with alphabetic suffices. 82A, 83A, 85 A left=ventral view, right=dorsal view. 85B=lateral view (v, d=dorsal and ventral sides). Other figures show gonostylus with subapical dilation viewed at maximum width. 84. *T. laeviceps* for comparison.

Descriptions and records

- 1) Synonymic lists cite only the original description, some important papers and those published after Schwarz (1939).
- 2) BL and WL₁ are given by ranges of measurements with up to ten specimens.

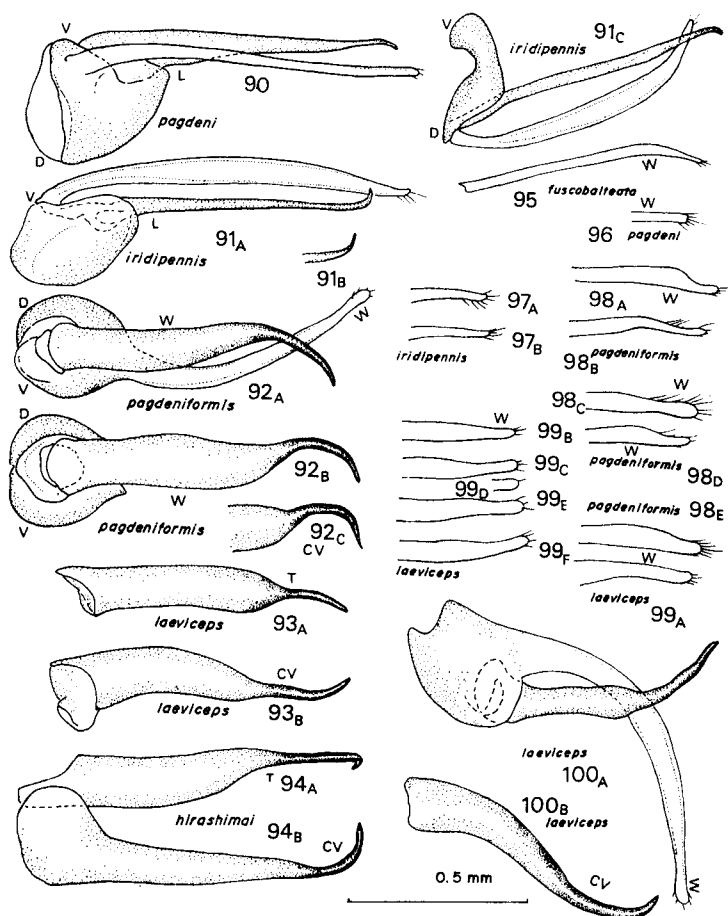


Figs. 86-89. Male genitalia of *T. laeviceps*, *pagdeniformis* and *T. iridipennis*. Left=ventral, right=dorsal view. Penis is drawn only in *T. iridipennis*.

3) Coloration is described in an abbreviated form. Full accounts are given by Schwarz (1939) for some species.

4) Collection data are shown with abbreviations given in Appendix at the end of the paper.

5) Holotype depository: *T. gressitti* sp. nov., Bernice P. Bishop Museum; *T. pagdeniformis* sp. nov., Entomological Laboratory, Kyushu University; All other new species, Zoological Institute, Hokkaido University.



Figs. 90–100. Partial views of male genitalia of some species. The same species is shown by the same numeral with alphabetic suffices. 90, 91A, 92A, 100A=lateral view, 91C posterior view, 92B ~ 94B and 100B=penis valve. 95~99F=gonostylus. v and d=dorsal and ventral sides, w=the indicated part viewed at its maximum width, L=base of penis valve viewed at its maximum width, cv=curvature viewed at its maximum, T=tapering viewed at its maximum.

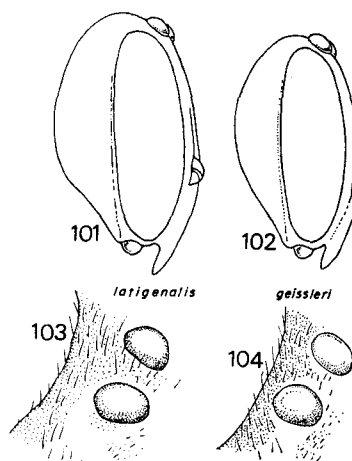
6) Abbreviations: L=length, W=width, T₇=Male metasomal tergum VII, S₅, S₆=Male metasomal sternum V and VI, w=worker.

***Trigona (Tetragonula) latigenalis* sp. nov.**

Trigona (Tetragonula) geisslieri, Yoshikawa, Ohgushi and Sakagami (nec Cockerell) 1969: 173 (partim).

Distinguished from other species by large size, wide gena and occiput. Melanic but clypeus often paler.

Worker (Pl. V, 1): BL 5.3~5.8 mm, WL₁ 5.8~6.1 mm, HW (Figs. 1, 2, Tab. 1) 2.3~2.4 mm, WL₂ (Figs. 1, 3, Tab. 2) 1.6~1.8 mm, HTL (Figs. 2, 3, Tab. 3) 2.2~2.4 mm. Black to blackish brown; antenna below testaceous, tegula, metasoma and legs predominantly dark (Tabs. 17~20) but clypeus and supraclypeus sometimes testaceous to pale ferruginous (Tab. 16). Anterior veins and stigma brown to testaceous. Hairs dark (Tab. 23~25); frontal hairs dark and not plumose (Tab. 22); mesoscutal hairs not well banded (Fig. 8), mesoscutellar fringe pale chocolate brown with blackish bristles (Tab. 24). WL₂/HW 0.75~0.80 (Figs. 1, 4, 6, Tab. 4), HTL/HW 1.00~1.05 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.35~1.45 (Figs. 3, 6, Tab. 6), EL/MOD small, 0.90~0.95 (Fig. 6, Tab. 7), LOD/MOD large, 0.75~0.85 (Figs. 4, 6, Tab. 8), IOD/OOD very small, 1.1~1.3 (Figs. 4, 6, Tab. 9), GW/EW extremely large 1.1~1.2 (Figs. 4, 6, 101, Tab. 10), ocelloccipital distance nearly as wide as ocellar diameter (Fig. 103), ML/FW very large, 0.4~0.6 (Figs. 4, 6, Tab. 11), SC/EL 0.50~0.55 (Tab. 12), FL/FW large, 0.9~1.1 (Figs. 4, 6, Tab. 13), HTW/HTL 0.36~0.38 (Figs. 4, 5, 6, Tab. 14), HBW/HTW 0.50~0.65 (Fig. 6, Tab. 15).



Figs. 101~104. Head in profile (101, 102) and occiput-vertex area (103, 104) of *T. latigenalis* and *T. geissleri* (worker).

Specimens examined: Holotype. Frasers Hill-b, Malaya. Paratypes. MALAYA Kepong (1w), Ulu Langat (20w), Gombak-c (2w), Cameron Highland (4w); P. THAILAND Khaophapha-Khaochong (1w).

Formerly this species was confounded by me with *T. geissleri*. Distinction became possible by comparing it with worker specimens of the latter species taken from a nest in Singapore (cf, below) accompanied by males. *T. latigenalis* is the largest species so far known of the subgenus, clearly distinguished by its absolute size from two next large dark species, *T. geissleri* and *T. hirashimai*. Wide gena and occiput, apparently correlated for each other are outstanding among all species studied. Supraclypeus is dark in some species while as pale as clypeus in others.

T. (T.) geissleri Cockerell

Trigona geissleri (Friese, nom. nud.) Cockerell 1918. Ann. Mag. Nat. Hist. (9) 2: 385.
Trigona confusella Cockerell 1919. Ann. Mag. Nat. Hist. (9) 3: 242; Schwarz 1937: 311.
Trigona (*Tetragona*) *geissleri*, Schwarz 1939. 117; Yoshikawa, Ohgushi and Sakagami

1969: 173 (partim).

Tetragonula geissleri, Moure 1961: 209.

Schwarz (1937, 1939) explained the controversies concerning this species as summarized below: 1) Friese named it *T. geissleri* but did not publish the description. 2) Cockerell (1918) assigned a male with black flagella from Sintang, N. Borneo, and some workers with ferruginous flagella from Singapore to *T. geissleri*. 3) Later, Cockerell (1919) obtained workers from Sintang and described *T. confusella* on the basis of Singapore workers. 4) Schwarz (1937) perceived some differences between workers from Sintang and Singapore, but considered both conspecific from the comparison with additional Bornean specimens. 5) Schwarz (1939) obtained six males of the size comparable to workers of *T. geissleri* from Malaya not accompanied by workers. One male (type A) had genitalia similar to that of *T. iridipennis* (= *T. laeviceps* in the present paper) while five (type B) had genitalia quite different. Veins and stigma were pale in type B and blackish in type A. Otherwise he found no difference. Referring to the description of *T. confusella*, which notes pale worker stigma and veins, Schwarz regarded type B as males of *T. geissleri*.

My interpretation of *T. geissleri* depends on worker and male specimens taken from the same nest in Singapore. Genitalia of these males well correspond to the description and illustration of type B by Schwarz (1939).

Large but distinctly smaller than T. latigenalis. Worker characterized by long hind tibia compared with T. hirashimai and zucchini of similar size. Male metasoma wider than head. Outer surface of male hind tibia flat but pilosity not uniform, admixing plumose hairs. Gonostylus very slender while penis valve robust and broad.

Worker: BL 4.8~5.0 mm, WL₁ 5.1~5.2 mm, HW 2.1~2.2 mm (Figs. 1, 2, Tab. 1), WL₂ 1.5~1.6 mm (Figs. 1, 3, Tab. 2), HTL 2.1~2.3 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below testaceous, sometimes brownish; clypeus, tegula, legs and metasoma variable but on the average moderately dark (Tabs. 16~20). Anterior veins and stigma testaceous to deep brown. Hairs dark (Tabs. 23~25); frontal hairs dark and not plumose (Tab. 22); mesoscutal hairs not well banded (Fig. 9); mesoscutellar fringe pale chocolate brown with blackish brown bristles (Tab. 24). WL₂/HW 0.7~0.8 (Figs. 1, 4, 6, Tab. 4), hind tibia long and wide, HTL/HW 1.05~1.10 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.45~1.55 (Figs. 3, 6, Tab. 6), EL/MOD 0.95~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.80 (Figs. 4, 6, Tab. 8), IOD/OOD 1.5~1.7 (Figs. 4, 6, Tab. 9), GW/EW 0.7~0.8 (Figs. 4, 6, 102, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (Fig. 104), ML/FW 0.2~0.4 (Figs. 4, 6, Tab. 11), SC/EL 0.5~0.6 (Tab. 12), FL/FW very large 1.0~1.1 (Figs. 4, 6, Tab. 13), HTW/HTL 0.34~0.35 (Figs. 4, 5, 6, Tab. 14), HBW/HTW 0.50~0.65 (Fig. 6, Tab. 15).

Male: BL 5.2~5.8 mm, WL₁ 5.2~5.4 mm, HW±2.0 mm (Figs. 1, 2, Tab. 1), WL₂±1.5 mm (Figs. 1, 3, Tab. 2), HTL relatively long, ±1.9 mm (Figs. 2, 3, Tab. 3). Coloration including veins generally as in worker, clypeus and tegula slightly darker but probably with considerable variation (Tabs. 16~20); scape and flagella below testaceous to ferruginous, the latter sometimes darker (Tab. 21).

Hairs dark (Tabs. 24~25); frontal hairs dark and not plumose (Tab. 22); erect occipital hairs $175\sim 200\ \mu$; mesoscutal hairs not well banded, homogenously short ($\pm 50\ \mu$), long hairs (to $100\ \mu$) very sparse; mesoscutellar fringe as in worker. WL_2/HW $0.75\sim 0.80$ (Figs. 1, 7, Tab. 4), HTL/HW large, $0.95\sim 1.05$ (Figs. 2, 7, Tab. 5), HTL/WL_2 $1.25\sim 1.35$ (Figs. 3, 7, Tab. 6). Seen frontally vertex relatively flat laterally, ocellar area rather abruptly raised. Facial contour rather transverse and eyes below relatively wide as in *T. hirashimai* (cf. Fig. 31). EL/MOD $1.10\sim 1.15$ (Fig. 7, Tab. 7), LOD/MOD $0.60\sim 0.70$ (Fig. 9, Tab. 8), SC/EL $0.40\sim 0.45$ (Tab. 12), FL/FW very large, $1.4\sim 1.5$ (Fig. 7, Tab. 13). Mandible normal (cf. Fig. 108). Maximum hair L of anterior and posterior margins of mid tibia and of posterior margin of mid basitarsus $150\sim 175\ \mu$, $150\sim 200\ \mu$, $200\sim 225\ \mu$; posterior mid tibial fringe with poor admixture of plumose hairs; L/L mid basitarsus/mid tibia ± 0.62 (Fig. 32). Hind tibia (Figs. 43, 50, 57) robust, HTW/HTL small $0.30\sim 0.32$ (Figs. 5, 7, Tab. 14); HBW/HTW $0.50\sim 0.55$ (Fig. 7, Tab. 15); outer surface flat, hairs relatively sparse especially anterioapically, with distinct admixture of plumose hairs postapically; posterior fringe with rich plumose hairs; hind basitarsus parallel-sided (Fig. 43), posterior margin gently curved; maximum hair L of posterior margins of both tibia and basitarsus $150\sim 175\ \mu$; ratio L/L hind basitarsus/hind tibia ± 0.37 , W/L hind basitarsus ± 0.47 .

Metasoma wider than head.¹⁾ T_7 (Figs. 62, 63) dorsapically not Y-ridged, apex distinctly pointed. S_5 (Fig. 71): antegladular area medially obsolete; postgladular area medially not differentiated, rather homogenously punctured and pubescent; apex semitransparent but not emarginate. S_6 (Fig. 78): Antecosta mildly curved, apodemal flexions broadly distant; apical process fairly long, basally half convergent, apical half parallel-sided, L/W about 34/6. Genitalia (Fig. 85): Gonostylus arising from lateral side of gonocoxite, basal half very slender ($25\ \mu$), apical half first gradually dilated (to $50\ \mu$) and suddenly tapering apically (to $15\ \mu$). Penis valve robust, as long as gonostylus, blade like, maximum W $180\sim 190\ \mu$ where lateral W $\pm 25\ \mu$, conspicuously curved, relatively wide till subapical part, apex sharply pointed.

Specimens examined: SINGAPORE Singapore-2 (57w 22♂ from the same nest); MALAYA Fraser's Hill-a (1w), -b (7w), Gombak-c (1w), Cameron Highland-b (2w), Penang-5a (1w); S. THAILAND Hua Hin (1w).

Male S_6 illustrated by Schwarz (1939) slightly differs from that of my specimens. Probably this reflects individual variation. His sixth male (type A cited above) with genitalia similar to that of *T. laeviceps* (his *iridipennis*) might be the male of *T. zucchini* described below. Schwarz (1939) recorded *T. geissleri* from various localities of Malaya and from Nan, N. Thailand. Whether this Thai specimen really be *T. geissleri* or possibly *T. hirashimai* described below requires critical study. The unique worker specimen from Hua Hin, S. Thailand, was in very poor condition,

1) Cockerell (1918) distinguished worker of *T. geissleri* from that of *T. valdezi* by broader metasoma. But in worker this difference is subtle.

but its size and proportions well coincide with Malayan specimens. This is the first authentic record of the species from Thailand.

***T. (T.) melina* Gribodo**

Trigona melina Gribodo 1893: Bull. Soc. Entom. Ital. 25: 262; Schwarz 1937: 316.

Trigona (Tetragona) melina, Schwarz 1939: 120.

Tetragonula melina, Moure 1961: 210.

In size and proportions HW/WL₂/HTL similar to T. geissleri. Easily distinguished from all other species by uniformly honey-testaceous coloration.

Worker: BL 5 mm, WL₁ 4.7~5.0 mm (4.5~5 and 5.5 mm in Schwarz 1939), HW 2.1~2.2 mm (Figs. 1, 2, Tab. 1), WL₂ 1.5~1.6 mm (Figs. 1, 3, Tab. 2), HTL 2.1~2.2 mm (Figs. 2, 3, Tab. 3). Including veins and stigma, concolorously honey-testaceous; apical terga somewhat deep toned. Hairs also pale testaceous to fulvous; frontal hairs not plumose; mesoscutal hairs not well banded. WL₂/HW 0.75~0.80 (Figs. 1, 4, 6, Tab. 4), HTL/HW relatively large, 1.05~1.10 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ less than in *T. geissleri*, ± 1.4 (Figs. 3, 6, Tab. 6), EL/MOD small, 0.95~1.00 (Fig. 6, Tab. 7), LOD/MOD relatively large, 0.75~0.80 (Figs. 4, 6, Tab. 8), IOD/OD small, ± 1.2 (Figs. 4, 6, Tab. 9), GW/EW fairly large, 1.0~1.1 (Figs. 4, 6, Tab. 10), ocellocipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.2~0.3 (Figs. 6, Tab. 11), SC/EL 0.50~0.60 (Tab. 12), FL/FW smaller than in *T. geissleri* 0.9~1.0 (Figs. 4, 6, Tab. 13), HTW/HTL 0.34~0.36 (Figs. 5, 6, Tab. 14), HBW/HTW 0.45~0.55 (Fig. 6, Tab. 15).

Specimens examined: MALAYA Gua Che Yatim (2w); P. THAILAND Ban Prakamp (1w, labelled "*T. melina* Gribodo, det. Schwarz").

In metric characters this species is close to *T. geissleri*, but GW/EW is larger and IOD/OD and FL/FW smaller. However, these differences require further confirmation as only three specimens were examined. Schwarz (1939) suggested variability in the hue of apical terga, which were slightly deeper than the rest of metasoma in all three specimens. One Malayan worker possessed dark brown flagella.

***T. (T.) hirashimai* sp. nov.**

? *Trigona geissleri*, Schwarz 1939 (nec Cockerell 1918): 117 (partim, specimen from Nan, N. Thailand).

As large as T. geissleri but in worker mesoscutal hairs pale and more or less well banded, mesoscutal fringe pale, hind tibia shorter and gena narrower; in male rather resembling T. laeviceps by simple hind tibia, rounded T₇, stouter gonostylus and horn like penis valve. Worker distinguished from T. zuehii and laeviceps by larger size, banded mesoscutal hairs, and male from T. laeviceps by S₅ medially broadly hairless and depressed, and gonostylus with subapical dilation.

Worker: BL 4.7~5.1 mm, WL₁ 4.9~5.3 mm, HW 2.1~2.2 mm (Figs. 1, 2, Tab. 1), WL₂ 1.3~1.6 mm (Figs. 1, 3, Tab. 2), HTL shorter than in *T. geissleri* 1.9~2.2 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below flavo-testaceous; clypeus and metasoma usually dark; tegula and legs frequently tending paler (Tabs. 16~20). Anterior veins and stigma testaceous to deep brown. Frontal hairs brownish but often paler and inconspicuously plumose (Tab. 22); mesoscutal hairs usually fulvous (Tab. 23), relatively well banded (Fig. 15); mesoscutellar fringe fulvous or sometimes paler, admixture of dark bristles scarce (Tab. 24); anterior corbicular hairs moderately dark (Tab. 25). WL₂/HW 0.70~0.75 (Figs. 1, 4, 6, Tab. 4), HTL/HW 0.95~1.00 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.35~1.45 (Figs. 3, 6, Tab. 6), EL/MOD 0.95~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.80 (Figs. 4, 6, Tab. 8), IOD/OOD 1.4~1.7 (Figs. 4, 6, Tab. 9), GW/EW relatively small, 0.6~0.8 (Figs. 4, 6, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW small among large species, 0.2~0.3 (Figs. 4, 6, Tab. 11), SC/EL 0.55~0.60 (Tab. 12), FL/FW 0.9~1.1 (Figs. 4, 6, Tab. 13), HTW/HTL 0.34~0.36 (Figs. 5, 6, Tab. 14), HBW/HTW 0.55~0.60 (Fig. 6, Tab. 15).

Male: BL 5.3~5.5 mm, WL₁ 4.8~5.2 mm, HW 1.9~2.1 mm (Figs. 1, 2, Tab. 1), WL₂ 1.3~1.4 mm (Figs. 1, 3, Tab. 2), HTL 1.6~1.8 mm, shorter than in *T. geissleri* (Figs. 2, 3, Tab. 3). Coloration as in worker (Tabs. 16~20); scape below mostly testaceous, flagella below usually paler (Tab. 21). Hairs relatively pale (Tabs. 23~25), frontal hairs often inconspicuously plumose (Tab. 22), erect occipital hairs long 225~250 μ ; mesoscutal hairs sparse, inconspicuously banded (Fig. 24), short hairs $\pm 75 \mu$, long hairs 150~175 μ ; mesoscutellar fringe pale as in worker (Tab. 24). WL₂/HW 0.70~0.75 (Figs. 1, 7, Tab. 4), HTL/HW 0.85~0.90 (Figs. 2, 7, Tab. 5), HTL/WL₂ 1.25~1.35 (Figs. 3, 7, Tab. 6). Facial contour rather transverse and eyes below relatively wide (Fig. 31); seen frontally, vertex flat laterally, rather abruptly raised medially; EL/MOD 1.10~1.20 (Fig. 7, Tab. 7), LOD/MOD 0.60~0.70 (Fig. 7, Tab. 8), SC/EL 0.40~0.45 (Tab. 12), FL/FW 1.1~1.3 (Figs. 7, Tab. 13). Mandible normal (Fig. 108). Maximum hair L of anterior and posterior margins of mid tibia and of posterior margin of mid basitarsus 150, 150 and 175 μ ; posterior midtibial fringe with poor admixture of plumose hairs; L/L mid basitarsus/mid tibia ± 0.54 (Fig. 33). Hind tibia (Figs. 5, 42, 56) distinctly smaller than in *T. geissleri*; HTW/HTL small 0.30~0.32 (Fig. 7, Tab. 14); HBW/HTW 0.50~0.65 (Fig. 7, Tab. 15); outer surface flat; hairs homogeneously dense and short, with no admixture of plumose ones both on surface and in posterior fringe (Figs. 42, 56); hind basitarsus parallel-sided; posterior margin basally gently outcurved, apically nearly straight; maximum hair L of posterior margin of hind tibia 100 μ , of hind basitarsus 125 μ ; ratio L/L hind basitarsus/hind tibia ± 0.35 , W/L hind basitarsus ± 0.48 .

Metasoma narrower than head. T₇ (Fig. 67) dorsapically not Y-ridged, apex broadly rounded. S₅ (Fig. 70): Antegladular area medially very short; post-gladular area medially widely depressed and sparsely haired; apex widely and roundly emarginate. S₆ (Fig. 77): Antecosta nearly straight, apodemal flexions

moderately distant; apical process fairly long, gradually tapering, L/W 40/10. Genitalia (Figs. 83, 94): Gonostylus arising from lateral side of gonocoxite; basal half gently tapering, maximum and minimum W 75 and 50 μ ; subapically sinuate and slightly dilated to 65 μ ; apical part about 80 μ , narrow (40 μ). Penis valve robust, horn like, slightly shorter than gonostylus, gradually tapering, about 180 μ wide at base and 125 μ at middle; apical part not conspicuously curved; apex slightly curved and pointed.

Specimens examined: Holotype (Worker). Chiang Dao-b, N. Thailand. Paratypes. N. THAILAND Doi Suthep-1a (1w), -1b (1w), -1c (4w), Doi Suthep-2 (2w, 62♂), Chiang Mai-2 (1w), Mae Klang (2w), Mae Fack-2 (1w), Mae Sa (1w), Lamphun (1w), Uthathani (1w). Further the following worker specimens in poor conditions are identified with *T. hirashimai* by size, proportions and pilosity (all from N. Thailand): Doi Suthep-1e (1w), Chiang Mai-2 (2w), Mae Klang (1w), Lamphun (1w), Fang 2b (1w).

The species is dedicated to Prof. Yoshihiro Hirashima, Entomological Laboratory, Kyushu University, Fukuoka.

This large species superficially resembles the sympatric species *T. pagdeni* by banded mesoscutal hairs, occasional appearance of plumose frontal hairs and pale hair coloration, but male hind legs and genitalia are similar to *T. laeviceps*. In worker, too, *T. hirashimai* is closer to *T. laeviceps* than *T. pagdeni*, e.g. in WL₂/HW (Tab. 4), HTL/HW (Tab. 5), EL/MOD (Tab. 7), IOD/OOD (Tab. 9), FL/FW (Tab. 13). *T. hirashimai* is also closer to *T. laeviceps* than *T. geissleri* of similar size by male hind tibia and genitalia as well as by some metric characters, e.g. WL₂/HW, GW/EW, FL/FW, etc. All so far known records are confined to N. Thailand. The single record of *T. geissleri* from Nan, N. Thailand, by Schwarz (1939) is likely to be of this species (cf. *T. geissleri*).

T. (T.) laeviceps Smith

Trigona laeviceps Smith 1857. Proc. Entom. Soc. Lond.: 93; Cockerell 1923. Ann. Mag. Nat. Hist. 9 (12): 241.

Trigona testaceicornis Cameron 1901 (nec Lepeletier 1836). Proc. Zool. Soc. 2: 36.

Trigona valdezi Cockerell 1918. Ann. Mag. Nat. Hist. 9 (9) II: 387; 1919. Phil. J. Sci. 14: 78, 79; Schwarz 1937: 309.

Trigona penangensis Cockerell 1919. Phil. J. Sci. 14: 78.

Trigona iridipennis, Schwarz 1937 (nec Smith 1854): 308.

Trigona (Tetragona) iridipennis var. *iridipennis*, Schwarz 1939 (nec Smith 1854) (partim): 111; Sakagami 1960: 147.

Trigona (Tetragona) iridipennis var. *valdezi*, Schwarz 1939: 116; 1951: 63; Sakagami and Yoshikawa 1961: 435.

Tetragonula laeviceps, Moure 1961: 208.

Tetragonula testaceicornis, Moure 1961: 208.

Tetragonula valdezi, Moure 1961: 208.

Trigona (Tetragona) iridipennis varr., Yoshikawa, Ohgushi and Sakagami 1969: (partim): 137.

This is the commonest *Tetragonula* species of medium size in S.E. Asia. Its nomenclatorial history is complicated and the taxonomic status is not yet completely solved. Schwarz (1939) regarded this as conspecific with *T. iridipennis*, originally described from Ceylon, and synonymized many later names, leaving a variety, *valdezi* Cockerell (type locality Singapore). Consequently, he recognized *T. iridipennis* var. *iridipennis* as a very ubiquitous form, extending from Ceylon and India via S.E. Asia to Solomon Islands. Moure (1961) mentioned that the specimens from Malaya are larger than those from India and proposed to use *T. laeviceps* (type locality, Mt. Ophir, S. Malaya) for the former. This proposition is followed in the present paper.

Actually the redefined *T. iridipennis* (India and Ceylon) is quite different from *T. laeviceps* (S.E. Asia) not only in size, but also in metric and pilosity characters in workers and various structural characters in males. It is strange why two competent specialists did not perceive such differences. Consequently, many earlier names synonymized by Schwarz with his *iridipennis* (= *iridipennis* + *laeviceps*) should be rechecked. The names published on the basis of Indian specimens may be synonymous with *T. iridipennis* and those for S.E. Asiatic specimens with *T. laeviceps* or partly with other species. The synonymic list presented above includes only plausible cases.

Next, distinction of *T. laeviceps* and *T. valdezi* is very difficult. The variation ranges of HW, WL_2 and HTL in Figs. 1~3 were prepared by combining all *laeviceps*- and *valdezi*-like specimens. The ranges are remarkably larger than in any other species. Partly this must depend on the number of available specimens much larger than in other species. But the inclusion of two good species is also not unlikely when the ranges are compared with those of *T. pagdeni*, which was also represented by many specimens. Schwarz (1937) first interpreted *T. valdezi* as slightly larger than *T. laeviceps* (=his *iridipennis*). Later (1939) he noted *T. valdezi* as "a slightly longer-winged variety of that species." It is uncertain he intended to stress whether wings of *T. valdezi* absolutely longer (=body size larger) or *T. valdezi* possessing relatively longer wings than *laeviceps*. Having examined about 600 specimens from various localities, I failed to distinguish these two forms by reliable characters, though a possible difference is not excluded for Malayan specimens. However, even if the two forms are distinct, they are certainly very close one another, sharing most diagnostic features. Therefore, the description covering both forms is given first, followed by variation analysis.

Medium sized. Basically dark colored. Distinguished from T. iridipennis group in worker by not well banded mesoscutal hairs and larger WL_2 and IOD/OOD , in male by simple hind tibia and gonostylus arising from lateral side of gonocoxite. At the larger extreme linked with T. zuchii in worker but WL_2/HW and GW/EW smaller and mesoscutal bristles paler. At the smaller extreme, linked with T. pagdeniformis, but distinguished in worker by not well banded mesoscutal hairs and in male by apical part of penis valve rather gently curved and apex of gonostylus gently tapering. Nearly identical with T. sarawakensis in size and in most proportions,

but uniformly dark, not provided with distinct pale parts.

Worker (Plate V, Figs. 2~4): Size quite variable, BL 4.0~4.6 mm (extremes 3.4 and 4.9), WL₁ 4.5~4.8 mm (extremes 3.7 and 5.0), HW 1.8~2.0 mm (Figs. 1, 2, Tab. 1), WL₂ 1.2~1.4 mm (Figs. 1, 3, Tab. 2), HTL 1.7~1.9 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below pale testaceous, flagella sometimes slightly darker; clypeus, legs and metasoma usually dark (Tabs. 16, 19, 20), fore trochanter testaceous to dark brown (Tab. 18); tegula highly variable, usually dark or blackish brown but often paler (Tab. 17). Anterior veins and stigma dark to blackish brown, rarely paler. Frontal hairs dark, not plumose (Tab. 22); mesoscutal hairs testaceous or fulvous, mixture of dark hairs scarce (Tab. 24), not well banded (Figs. 11~13); mesoscutellar fringe fulvous to pale testaceous, stouter bristles mainly pale testaceous to brown, but occasionally dark brown (Tab. 24); anterior corbicular bristles moderately to fairly dark (Tab. 25). WL₂/HW 0.7~0.8 (Figs. 1, 4, 6, Tab. 4), HTL/HW 0.95~1.05 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.30~1.50 (Figs. 3, 6, Tab. 6), EL/MOD 0.95~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.80 (Figs. 4, 6, Tab. 8), IOD/OOD 1.4~1.7 (Figs. 4, 6, Tab. 9), GW/EW 0.6~0.8 (Figs. 4, 6, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.2~0.4 (Figs. 4, 6, Tab. 11), SC/EL 0.50~0.60 (Tab. 12), FL/FW 0.8~1.0 (Figs. 4, 6, Tab. 13), HTW/HTL 0.34~0.38 (Figs. 5, 6, Tab. 14), HBW/HTW 0.55~0.65 (Fig. 6, Tab. 15).

Male: BL 4.1~4.8 mm, WL₁ 4.4~4.7 mm, HW 1.7~1.8 mm (Figs. 1, 2, Tab. 1), WL₂ 1.1~1.3 mm (Figs. 1, 3, Tab. 2), HTL 1.4~1.5 mm (Figs. 2, 3, 5, Tab. 3). Coloration as in workers (Tabs. 16~20); flagella below mostly dark (Tab. 21). Frontal hairs not plumose (Tab. 22), fulvous to dark brown; erect occipital hairs 170~200 μ ; mesoscutal hairs sparse, pale, not well banded (Fig. 25), short hairs 50 μ , long hairs 75~100 μ ; mesoscutellar fringe pale as in worker (Tab. 24). WL₂/HW ± 0.7 (Figs. 1, 7, Tab. 4), HTL/HW ± 0.85 (Figs. 2, 7, Tab. 5), HTL/WL₂ small, less than 1.25 (Figs. 3, 7, Tab. 6). Facial contour as in *T. hirashimai*, vertex relatively flat (cf. Fig. 31); EL/MOD 1.10~1.15 (Tab. 7), LOD/MOD ± 0.60 (Fig. 7, Tab. 8), SC/EL 0.35~0.45 (Tab. 12), FL/FW ± 1.1 (Fig. 7, Tab. 13). Mandible normal (cf. Fig. 108). Maximum hair L of anterior and posterior margins of mid tibia and mid basitarsus and of posterior margin of mid basitarsus 100, 100, 150 μ ; posterior midtibial fringe with poor admixture of plumose hairs (Fig. 35); L/L mid basitarsus/mid tibia 0.64. Hind tibia similar to *T. hirashimai* except size (Figs. 5, 44); HTW/HTL 0.36~0.40 (Figs. 5, 7, Tab. 14), HBW/HTW 0.55~0.60 (Fig. 7, Tab. 15); outer surface flat, hairs homogenously dense and short, with no admixture of plumose ones both on surface and posterior fringe (Figs. 44, 58). Hind basitarsus (Fig. 44) nearly parallel-sided; posterior margin imperceptibly outcurved; maximum hair L of posterior margin of tibia and basitarsus 75, 75~100 μ ; W/L hind basitarsus ± 0.50 .

Metasoma narrower than head. T₇ (Fig. 68) dorsapically not Y-ridged, apex rounded. S₅ similar to *T. iridipennis* (cf. Fig. 73); antegladular area medially relatively long; postgladular area relatively short; median depression small,

apex narrowly and shallowly incised. S_6 (Fig. 74): Antecosta nearly straight, apodemal flexions moderately distant; apical process moderately long, narrowly triangular, apex variable but generally tapering, L/W about 30/8. Genitalia (Figs. 84, 86, 93, 99, 100): Gonostylus arising from lateral side of gonocoxite, not exceeding penis valve; basal half relatively wide ($135\ \mu$), apically gradually tapering and sinuate; apical part narrow ($35\ \mu$), apex imperceptibly dilated ($40\ \mu$). Penis valve horn like $\pm 130\ \mu$ at base, $60\ \mu$ at middle, rather suddenly tapering at apical 1/3; apical part gently curved; apex not too much pointed.

Specimens examined: SINGAPORE Singapore-1 (11w), -2 (100w), -4 (1w); MALAYA Subang (2w), Kepong (1w), Ulu Langat (1w), Kuala Lumpur-3e (1w), -3d (7w), -3e (1w), -3f (1w), -3g (1w), -3a (1w), -3b (1w), -3h (1♂), Gombak-a (1w), -b (23w), -c (14w), -e (8w), Templer Park-a (1w), Fraser's Hill-a (2w), -b (3w), -c (7w), Fentung Sempak-a (27w, 9♂), -b (50w), Taman Negara (19w), Kuala Tahan-a (17w), -b (1w), -c (14w), Gua Che Yatim (1w), Kuala Tranggan (12w), Bagan Tiang-a (1w), Tahan River (1w), Pulan Jarak-a (1w), -b (1w), Bukit Mertajam (3w), Penang-1a (4w), -1b (4♂), -1c (1w), -1d (1w), -1e (1w), -4 (1w), -5a (1w); P. THAILAND Songkhla-b (1w), -c (1w), Khao Chong-1 (1w), Trana (1w), Naborn (1w), Khaophappa-Khao Chong (97ww), Patalung (1♂), Banna (18ww); S. THAILAND Chantaburi/Prew-c (1w), -d (3w), -f (6w), -h (1w), -j (1w), Saraburi (3w); E. THAILAND Nakom Phanom (2w), Ubol (2♂); N. THAILAND Uthaithani (4w), Doi Suthep-a (13w), -b (4w), -d (1w), Chiang Mai-2 (3w), Chiang Dao (6w), Mae Fack-1 (3w), Muang Fang-a (6w), -b (3w), -c (1w), Fang-1a (8w), -1b (29w), -1c (8w), -2a (3w), -2b (7w), -3 (4w); VIET NAM Dai Lanh (42w), Kontum (2w), Pleiku-1 (2w), -2 (1w), -3 (1w), Ban Me Thout (12w), Dak Song (4w), Dalat-1a (1w), -1b (1w), -2 (1w), -3 (1w), -4 (1w), Fyan-a (3w), -b (3w), Di Linh-1a (3w), -1b (13w), -2 (3w), Phan Rang (1w), Karyu Danar (2w), Phan Thiet (2w), Balao-1a (16w), -1b (6w), -2 (6w); LAOS Muong Sing (3w), Luang Prabang (5w), Paksane (2w).

As already mentioned the body size of *T. laeviceps* is highly variable. Four extreme cases are cited, in which HW of smaller specimens is only 84% of larger ones:

Provenance and Specimen No.	BL (mm)	WL ₁ (mm)	HW (40=1 mm)	WL ₂ (40=1 mm)
Nakom Phanom (E. Thailand), A-2	4.50	4.68	83	60
Dai Lanh (Viet Nam), A-1	4.87	5.06	"	58
Fentung Sempak (Malaya), Y-1	3.88	4.12	68	49
Taman Negara (Malaya), Y-16	3.44	3.77	"	45

Table 26 shows size distribution of HW and WL₂ in the localities where ten or more specimens were collected. The difference is fairly large among these, e.g. between Kuala Tahan and Dai Lanh.

Variations of body size in different areas are presented in Fig. 105 by relation WL₂/HW. Graph A gives the variation in males from different localities. A single male from Kuala Lumpur (black circle) labelled "*T. iridipennis* det. Schwarz" is very small. Males from Fentung Sempak, Malaya, are generally smaller than others, but the relation is not strictly isomorphic, Fentung Sempak males possessing wing slightly longer relative to HW. No essential structural differences occur among these males. Apex of gonostylus exhibits some subtle

Table 26. Size variation of *T. laeviceps* workers in some localities where 10 or more specimens were collected. Except for Singapore, the specimens from the same locality by different collectors were combined (cf. Appendix)

Localities	N	Size by micrometer scale (40=1 mm)																			
		HW WL ₂	68 45	69 46	70 47	71 48	72 49	73 50	74 51	75 52	76 53	77 54	78 55	79 56	80 57	81 58	82 59	83 60	84 61		
SINGAPORE																					
Singapore-3	100								4	14	35	27	18	2							
	100						2	14	27	30	23	4									
Singapore-1	11											4	4	3							
	11								1	1	3	5	1								
MALAYA																					
Fentung Sempak	69		1		1	2	8	9	17	21	9	1									
	69						2	4	4	12	16	18	10	3							
Frasser's Hill	14					1	2	2	2	1	2	1	1	1		1					
	14							1	1	1	5	1	1	4							
Gombak Reserve	47			1	7	6	6	11	4	8	1	2	1								
	45					4	5	8	5	5	5	10	3								
Kuala Tranggan	12		1	3		3				1	2	1	1								
	10			1		2		1	1	2	2		1								
Kuala Tahan	31				4	4	9	2	8	4											
	30				1	1	6	7	8	3	3	1									
Taman Negara	26		2	1		3	1	4	3	5	5	1	1								
	26		2	1					5	3	8	5	2								
Kuala Lumpur	11				1		3	3		2	2										
	11					3	2	1	1	3	1										
Penang	9					1	1				1	4	1			1					
	9					1		1		1	2	3	1								
PENINSULAR and S. THAILAND																					
Khaophappa-Khaochong	90				11	10	16	14	4	7	7	9	3	5	4						
	89			1	1	6	26	11	10	13	6	8	5	2							
Banna	18							3	4	5	1	3	2								
	18						1	4	5	4	2	2									
Chantaburi and Prew	12								1	2	3	2	1		2		1				
	12							3	1	4	1	1	1	1							
VIET NAM																					
Ban Me Thout	11								2	2	6	1									
	13				2					3	2	4	2								
Dai Lanh	35					1						2	3	3	8	6	6	5	1		
	35									3	2	1	3	5	3	14	2	2			
Dalat and Fyan	12							1	3	5	1	1	1								
	12									4	4	2	1	1							
Di Linh	18					1		3	8	2		1	1	1				1			
	18					1	2	4	4	3			1	1	2						

Table 26. (Continued)

Localities	N	Size by micrometer scale (40=1 mm)																			
		HW WL ₂	68 45	69 46	70 47	71 48	72 49	73 50	74 51	75 52	76 53	77 54	78 55	79 56	80 57	81 58	82 59	83 60	84 61		
Blao	22						3	2	2	3	7	3	2								
	20			1			5		2	6	5	1									
N. THAILAND																					
Fang	58									2	1	8	22	11		8	5	1			
	59							2	2	7	6	18	4	9		6	3	2			
Muang Fang	11											2	3	5			1				
	10							1				2	2	2		2	1				
Doi Suthep	17				1	1	1	2			3	3	4	1				1			
	18					1	2	1			1	3				1	6	2	1		

differences (Figs. 99). Apex of penis valve tapers more gradually in some specimens. Pigmentation of the apical half of penis valve varies among specimens from jet black to brownish. All these can be considered mere intraspecific variations, just like some differences seen between the illustrations of *S₆* and genitalia by Schwarz (1939, Figs. 7B and 8B) and by myself (Figs. 74, 86).

For workers two samples were chosen as a basis of comparisons: FS: Workers collected on flowers in Fentung Sempak, Malaya, possibly of relatively homogenous nature, and SG: Workers taken from two nests built 50 cm apart for each other in window frames of the University of Singapore (=Singapore-3). Two samples were isomorphic as to HTL/WL₂ and HTL/HW where SG was on the average larger. Relation WL₂/HW is given in Fig. 105 B, together with the following workers in the collection of American Museum of Natural History, all determined by Schwarz himself, three "*iridipennis*" (L₁-L₃) and three "*valdezi*" (V₁-V₃). One worker from Solomon Is. in the collection of British Museum and identified with *T. iridipennis* is also added to (V₄). Interestingly, all these specimens lie outside the size ranges of FS and SG, "*iridipennis*" much smaller than FS and "*valdezi*" larger in HW than SG. Between FS and SG a relation somewhat allomorphic as found between Fentung Sempak and Penang males (cf. graph A) is suggested. If this relation is consistent, the following interpretation could be held: FS=*laeviceps* (= *iridipennis* by Schwarz) and SG=*valdezi*, and *valdezi* is, contrary to the statement by Schwarz, relatively "short winged".¹⁾

In order to find such segregation, WL₂/HW relation was plotted in graphs C~I various areas and some localities separately. The size ranges of FS, SG and all examined specimens (cf. Fig. 1) are added to each graph. Contrary to expectation,

1) The name *valdezi* first appeared in 1918, then in 1919 again as a new species. The features regarded by Cockerell as specific are, somewhat dusky wings, ferruginous tegula, brown abdomen, black femora, tibiae and mid and hind basitarsi. None of these are stable in the specimens examined by me.

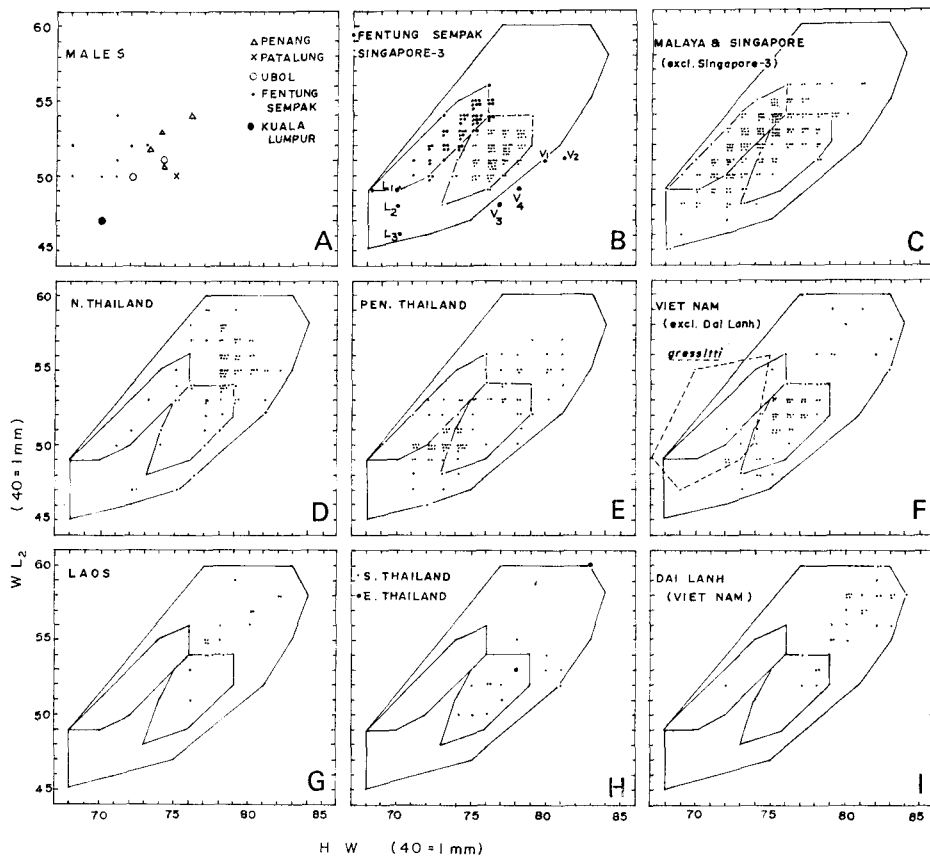


Fig. 105. WL_2/HW relation in *T. laeviceps*. A. Males. B~I. Workers from different areas. In B~I size ranges of FS (Fentung Sempak), SG (Singapore-3) and of all workers measured are shown by polygons. In F size range of *T. gressitti* is added to. In B, $L_1 \sim L_3$ = workers identified with "*iridipennis*" by Schwarz (Provenance, L_1 = Tahan River, L_2 = Kuala Lumpur, L_3 = Java), $V_1 \sim V_3$ = workers identified with *valdezi* by Schwarz (Provenance, V_1 = Amboina, V_2 = Caroline Is., V_3 = Mindanao), V_4 = worker from Solomon Is. identified with *T. iridipennis* by Krombein.

no clear segregation was obtained. The specimens from Peninsular Thailand show a vague segregation (cf. also Tab. 26, Khaophappa-Khao Chong) but rather isomorphically. Those from Viet Nam are heterogenous, involving fairly large ones (mostly from Dai Lanh, graph I) and medium sized ones. Outside of Malaya the size range of FS tends to be occupied less than that of SG. This tendency is particularly clear in Viet Nam and, though the specimens are insufficient, in S. and E. Thailand. Another more evident tendency is an approximately isomorphic increase of body size from southern to northern areas. This is suggested in Table

Table 27. Size difference of *T. laeviceps* workers among various areas

HW in micrometer scale (40=1 mm). *=converted to mm in parentheses																				
Areas	$\bar{x}$ *	SD*	N	Frequency distribution																
				68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Singapore-3 (from a nest)	76.3838 (1.9096)	1.1609 (0.0290)	99								4	14	35	27	18	1				
Malaya+Sin- gapore (excl. Singapore-3)	73.9075 (1.8477)	2.5318 (0.0633)	227	3	4	14	18	32	31	29	38	22	15	13	6	1	1			
Peninsular Thailand	74.8393 (1.8710)	2.9446 (0.0736)	112	2	2		11	11	19	14	8	8	9	14	5	5	4			
Southern Thailand	77.6667 (1.9417)	2.4404 (0.0610)	15							1	2	3	3	1		2	2	1		
Eastern Thailand			2												1				1	
Viet Nam	77.2455 (1.9311)	3.1194 (0.0780)	110					6	4	10	18	16	12	8	6	9	6	7	7	1
Northern Thailand	78.0583 (1.9515)	2.1308 (0.0533)	103				1	1	2	3	4	5	16	31	19	10	7	1	3	
Laos	78.4000 (1.9600)	1.4318 (0.0358)	10									2		3	2	3				

WL ₂ in micrometer scale (40=1 mm). *=converted to mm in parentheses																			
Areas	$\bar{x}$ *	SD*	N	Frequency distribution															
				45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Singapore-3 (from a nest)	51.6400 (1.2910)	1.2126 (0.0303)	100							2	14	27	30	23	4				
Malaya+Singa- pore (excl. Singapore-3)	52.0723 (1.3018)	2.2311 (0.0558)	235	2	2	1	13	15	24	28	33	46	45	19	7				
Peninsular Thailand	51.6134 (1.2903)	2.2346 (0.0559)	119		1	2	3	7	35	16	15	16	8	9	5	2			
Southern Thailand	52.2857 (1.3071)	1.7496 (0.0437)	14						3	1	5	2	1	1	1				
Eastern Thailand			2										1						1
Viet Nam	53.7963 (1.3449)	3.0905 (0.0773)	108		1		3	6	3	8	21	17	8	7	9	4	16	2	3
Northern Thailand	54.7596 (1.3690)	2.5888 (0.0647)	104				1	1	6	3	9	8	24	10	14	9	13	5	1
Laos	55.1000 (1.3775)	2.2561 (0.0564)	10							1		2	1	1	2	2		1	

26, but more clearly in Table 27. The number of records of "*iridipennis*" and "*valdezi*" by Schwarz (1939, 1961) coincides to some degree with this tendency:

	Malaya	Thailand	Viet Nam	Cambodia
<i>iridipennis</i>	31	1	1	
<i>valdezi</i>	22	5	1	1

Possibly he identified larger specimens with *valdezi*, which are more abundant in Thailand and Indochina. A temporizing solution may be to identify small specimens from Malaya with *T. laeviceps* and larger ones from Malaya and all specimens from other areas with *T. valdezi*. At the present, however, there is no way to distinguish these two forms by body size, nor by any other characters. Therefore, all examined specimens are, for the time being, identified with *T. laeviceps*, a species highly variable in size. The distributional range of this species is not limited to the Continental S.E. Asia. It certainly extends to Malay Archipelago and further eastward, as suggested by the male of "*iridipennis*" from Solomon Is., genitalia of which were illustrated by Schwarz. In this connection, it is noteworthy that all four extra-continental specimens cited in Fig. 105 B as *V.* stand outside the size range of SG, exhibiting a super-SG tendency. Whether or not this indicates the occurrence of another, relatively short winged form in Malay Archipelago and Pacific areas, possibly involving the population of Singapore, is left for further studies.

T. (T.) zucchini sp. nov.

? *Trigona* (*Tetragona*) *geissleri*, Schwarz 1939: 117 (partim).

Trigona (*Tetragona*) *iridipennis* varr. Yoshikawa, Ohgushi and Sakagami 1969: 173 (partim).

Size intermediate between T. geissleri and large specimens of T. laeviceps. Distinguished from T. geissleri by shorter hind tibia, from T. laeviceps by wider gena and darker mesosomal hairs.

Worker: BL 4.4~5.2 mm, WL₁ 4.9~5.3 mm, HW 2.0~2.1 mm (Figs. 1, 2, Tab. 1), WL₂ 1.4~1.7 mm (Figs. 1, 3, Tab. 2), HTL 1.8~2.0 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; clypeus, tegula, legs and anterior metasomal terga occasionally paler (Tabs. 16~20). Anterior veins and stigma dark to blackish brown. Frontal hairs dark, not plumose (Tab. 22); mesoscutal hairs not well banded, dark brown with few admixture of pale hairs (Tab. 23); mesoscutellar fringe testaceous to brownish with abundant admixture of dark hairs (Tab. 24); anterior corbicular bristles fairly dark (Tab. 25). WL₂/HW larger than in *T. laeviceps* 0.75~0.80 (Figs. 1, 4, 6, Tab. 4), HTL/HW as in *T. laeviceps*, 0.95~1.05, distinctly smaller than in *T. geissleri*, HTL/WL₂ 1.25~1.35 (Figs. 3, 6, Tab. 6), EL/MOD 0.95~1.05 LOD/MOD 0.75~0.80 (Figs. 4, 6, Tab. 7), IOD/OOD 1.3~1.6 (Figs. 4, 6, Tab. 9), GW/EW 0.8~1.0, larger than in *T. laeviceps* (Figs. 4, 6, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.3~

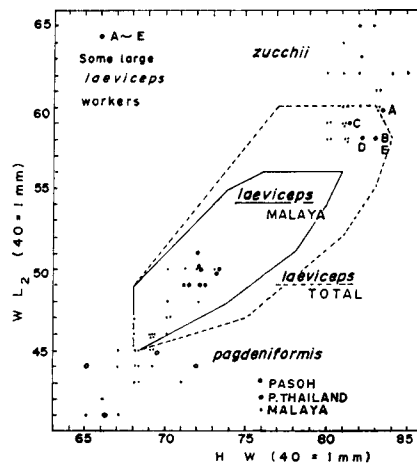
0.4 (Figs. 4, 6, Tab. 11), SC/EL 0.50~0.60 (Tab. 12), FL/FW a little larger than in *T. laeviceps*, 0.9~1.1 (Figs. 4, 6, Tab. 13), HTW/HTL 0.36~0.38 (Figs. 5, 6, Tab. 14), HBW/HTW 0.55~0.65 (Fig. 6, Tab. 15).

Specimens examined: Holotype (Worker). Fraser's Hill-b, Malaya. Paratypes. MALAYA Fraser's Hill-b (8w), -c (1w), Cameron Highland-a (1w), -b (7w), Gombak-d (1w), Penang-5b (1w), Templer Park-b (10w from the entrance of one nest), -c (7w).

The species is dedicated to Dr. Ronaldo Zucchi, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, my lasting co-worker in meliponology.

This species was separated as a byproduct of the examination of numerous Malayan specimens of *T. laeviceps* and comparison of these with *T. geissleri*. The relation with *T. geissleri* is visualized in Figs. 1~3. WL_2/HW does not much differ from each other while HTL is distinctly shorter in *T. zucchii*. Further, anterior veins and stigma are much darker. As mentioned in *T. geissleri*, one male cited Schwarz, which was same sized with *T. geissleri* but had darker veins and genitalia similar to that of *T. laeviceps*, is possibly the male of *T. zucchii*. From another large species, *T. hirashimai* in N. Thailand, *T. zucchii* is easily distinguished by not well banded mesoscutal hairs, darker veins and stigma, larger WL_2/HW (Figs. 1, 4, 6, Tab. 4) and GW/EW (Figs. 4, 6, Tab. 10).

Fig. 106. WL_2/HW relation (worker) in *T. laeviceps*, *zucchii* and *pagdeniformis*. Size range of *T. laeviceps* given by two polygons. Solid=range of Malayan specimens (cf. Fig. 105, C), Broken=range of all specimens (cf. Fig. 105B~I and also Fig. 1). A~E are some large *T. laeviceps* workers explained in the text.



The distinction from *T. laeviceps* is more difficult. As given in Fig. 106 variation ranges of WL_2/HW of both species overlap when all specimens of *T. laeviceps* are combined, but not when only the sympatric Malayan specimens of *T. laeviceps* are compared. Mesosomal hairs of most Malayan *laeviceps* specimens are basically pale with few admixture of dark hairs. Some non-Malayan *laeviceps* specimens attaining the size of *T. zucchii* are given in Fig. 106 with alphabets. These are A. Nakom Phanom (E. Thailand) A-2, B~D. Dai Lanh (Viet Nam) A-1, 3, 4, E.

Phan Thiet (Viet Nam) A-1. These specimens were intermediate in most metric characters but all possessed fairly pale mesoscutal and mesoscutellar hairs (degree II~III). For the time being, these are regarded as extremely large specimens of *T. laeviceps*.

Another feature which favors the recognition of *T. zucchini* as an independent species is ethological. The entrance of one nest, from which ten workers were captured (Templer Park-b) was very characteristic (Plate V, Fig. 8). The entrance was expanded at the periphery, somewhat irregularly funnel shaped, and the peripheral margin was ornamented with moniliform deposition of bright yellow resin. No such elaborated entrance was found in two colonies of *T. laeviceps* from Singapore (Singapore-3, Kawamichi, pers. comm.) nor in other *Tetragonula* nests (Sakagami et al. unpub., partly given in Yoshikawa, Ohgushi and Sakagami 1969). Dr. M. Nadchatram of Institute for Medical Research told me that he has encountered several times with such ornamented nest entrance in forests near Kuala Lumpur. The importance of nest entrance structure for stingless bee taxonomy was also stressed by Moure (1961, p. 207, cf. also Kerr et al. 1967, Wille and Michener 1973).

T. (T.) sarawakensis Schwarz

Trigona sarawakensis Schwarz 1937: 113.

Trigona (Tetragona) sarawakensis var. *sarawakensis*, Schwarz 1939: 106; Sakagami 1959: 119.

Trigona (Tetragona) sarawakensis var. *dresheri* Schwarz 1939: 106; Yoshikawa, Ohgushi and Sakagami 1969: 174.

Size and body proportions as in T. laeviceps, but showing marked flavinism of clypeus, tegula, metasoma and legs.

Worker: BL 4.4~4.5 mm, WL₁ 4.4~4.6 mm, HW $\pm$ 1.9 mm (Figs. 1, 2, Tab. 1), WL₂ $\pm$ 1.3 mm (Figs. 1, 3, Tab. 2), HTL $\pm$ 1.8 mm (Figs. 2, 3, Tab. 3). Head and mesosoma above blackish, occasionally with some chestnut tint; antenna below, clypeus (Tab. 16), supraclypeus and tegula (Tab. 17) testaceous to ferruginous; mesosomal sides blackish brown to deep chestnut; metasoma ferruginous or chestnut brown, apical terga occasionally slightly darker (Tab. 18); legs deep brown to ferruginous (Tabs. 19, 20); femora, tibiae and basitarsi occasionally darker to blackish or with black stripes. Anterior veins and stigma brownish. Frontal hairs fulvous to testaceous, not plumose (Tab. 22); mesoscutal hairs not well banded (Fig. 10), fulvous to testaceous with no or few admixture of dark hairs (Tab. 23); mesoscutellar fringe fulvous to testaceous without admixture of dark bristles (Tab. 24); anterior corbicular bristles moderately to fairly dark (Tab. 25). WL₂/HW 0.70~0.75 (Figs. 1, 4, 6, Tab. 4), HTL/HW 0.95~1.00 (Figs. 3, 6, Tab. 5), HTL/WL₂ 1.35~1.45 (Figs. 3, 6, Tab. 6), EL/MOD 1.00~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.80 (Figs. 4, 6, Tab. 8), IOD/OOD 1.5~1.6 (Figs. 4, 6, Tab. 9), GW/EW 0.6~0.8 (Figs. 4, 6, Tab. 10), ocelloccipital distance about

1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.2~0.4 (Figs. 4, 6, Tab. 11), SC/EL 0.50~0.55 (Tab. 12), FL/FW 0.8~1.0 (Figs. 4, 6, Tab. 13), HTW/HTL 0.36~0.38 (Figs. 5, 6, Tab. 14), HBW/HTW 0.55~0.60 (Fig. 6, Tab. 15).

Specimens examined: SINGAPORE Singapore-5 (1w); MALAYA Tapah (10w from a nest), Bagan Tiang-b (1w).

This species was first described from Sarawak (Schwarz 1937), and later recorded from Thailand, N. Borneo, Java (Schwarz 1939), Singapore (Sakagami 1959) and Malaya (Yoshikawa et al. 1969). The above description was mainly made based upon the specimens collected from a nest in Tapah, which coincided with the description by Schwarz. As seen in Figs. 1~6 and Tabs. 1~15, *T. sarawakensis* is isomorphic with large specimens of *T. laeviceps* in most size and proportion characters. Schwarz (1937) gave an illustration of worker mandible with the apex rather rounded (Pl. II, Fig. E), not bluntly pointed as in *T. laeviceps* (=his *iridipennis*, Pl. III, Fig. H). All *Tetragonula* species examined by me have rather pointed mandible, so that his illustration seems erroneous. Therefore, the unique difference of *T. sarawakensis* from *T. laeviceps* is its paler coloration. At the present, *T. sarawakensis* is treated as an independent species, as its coloration deviates fairly well from the variation range of *T. laeviceps*. Schwarz (1939) described var. *dresheri* from Middle and Eastern Java, possessing dark stripes on femora, fore and fore and mid tibiae, and hind tibia black except fulvous spot. The presence of such local population is possible, but coloration of legs of the specimens taken from the same nest in Tapah varied considerably, on the average, showing a condition intermediate between *sarawakensis* and *dresheri*. Here var. *dresheri* is treated as a mere color variant.

T. (T.) pagdeniformis sp. nov.

Belonging to T. laeviceps group by metric characters, male hind tibia and genitalia, but smaller, mesoscutal hairs well banded and male gonostylus slightly dilated subapically. From T. pagdeni and iridipennis with similar size and banded mesoscutal hairs distinguished by male characters and in worker by larger WL₂/HW, HTL/HW and EL/MOD.

Worker: BL 3.5~4.1 mm, WL₁ 3.9~4.5 mm, HW 1.7~1.8 mm (Figs. 1, 2, Tab. 1), WL₂ 1.1~1.2 mm (Figs. 1, 3, Tab. 2), HTL 1.6~1.7 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below testaceous to ferruginous; clypeus, tegula, legs and metasoma on the average relatively dark (Tabs. 16~20). Anterior veins and stigma dark to blackish brown. Frontal hairs fulvous to whitish, not plumose (Tab. 22); mesoscutal hairs fulvous to pale testaceous (Tab. 23), generally sparser than in *T. laeviceps*, though less than in *T. iridipennis* group, more or less well banded (Figs. 16~18); mesoscutellar fringe fulvous to pale testaceous, with admixture of deep to dark brown bristles (Tab. 24); anterior corbicular bristles moderately to fairly dark (Tab. 25). WL₂/HW 0.65~0.75 (Figs. 1, 4, 6, Tab. 4), HTL/HW 0.95~1.05 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.40~1.50 (Figs. 3, 6, Tab.

6), EL/MOD 1.00~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.75 (Figs. 4, 6, Tab. 8), IOD/OOD 1.5~1.8 (Figs. 4, 6, Tab. 9), GW/EW 0.6~0.8 (Figs. 4, 6, Tab. 10), ocell-occipital distance 1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.1~0.3 (Figs. 4, 6, Tab. 11), SC/EL small 0.50~0.55 (Tab. 12), FL/FW 0.7~0.9 (Figs. 4, 6, Tab. 13), HTW/HTL 0.32~0.36 (Figs. 5, 6, Tab. 14), HBW/HTW 0.5~0.6 (Fig. 6, Tab. 15).

Male: BL 4.0~4.4 mm, WL 4.2~4.4 mm, HW 1.7~1.8 mm (Figs. 1, 2, Tab. 1), WL₂ 1.2~1.3 mm (Figs. 1, 3, Tab. 2), HTL shorter than in *T. iridipennis* and *pagdeni* 1.4~1.5 mm (Figs. 2, 3, Tab. 3). Coloration as in worker (Tab. 16~20); scape and flagella below darker, often dark brown (Tab. 21). Frontal hairs not plumose (Tab. 22); erect occipital hairs 175~200 μ ; mesoscutal hairs sparse, obscurely banded (Fig. 27), short hairs 50 μ , long hairs 75~100 μ ; mesoscutellar fringe pale as in worker with testaceous to dark brown bristles (Tab. 24). WL₂/HW 0.70~0.80 (Figs. 1, 7, Tab. 4), HTL/HW 0.80~0.90 (Figs. 2, 7, Tab. 5), HTL/WL₂ small, less than 1.25 (Figs. 3, 7, Tab. 6). Facial contour as in *T. hirashimai* (cf. Fig. 31), vertex relatively flat; EL/MOD 1.15~1.20 (Tab. 7), LOD/MOD 0.60~0.65 (Fig. 7, Tab. 8), SC/EL 0.40~0.45 (Tab. 12), FL/FW 1.0~1.2 (Fig. 7, Tab. 13). Mandible normal (cf. Fig. 108). Hair L of anterior and posterior margins of mid tibia and of posterior margin of mid basitarsus 125, 125, 160 μ ; posterior midtibial fringe with poor admixture of plumose hairs (Fig. 36); L/L mid basitarsus/mid tibia 0.62. Hind tibia similar to *T. laeviceps* (Figs. 5, 40) but HTW/HTL smaller 0.28~0.34 (Figs. 5, 7, Tab. 14); HBW/HTW 0.55~0.65 (Fig. 7, Tab. 15); outer surface flat; hairs homogeneously dense and short, with no admixture of plumose ones both on surface and in posterior fringe (Figs. 40, 48, 54); hind basitarsus (Fig. 40) nearly parallel-sided; posterior margin gently outcurved; maximum hair L of posterior margin of hind tibia 75~100 μ , of hind basitarsus 75~80 μ ; W/L hind basitarsus ± 0.5 .

Metasoma narrower than head. T₇ (Fig. 64), dorsapically not Y-ridged, apex mildly pointed. S₅ similar to *T. iridipennis* (cf. Fig. 73); antegladular area medially relatively short; postgladular area relatively short, median depression small, apex narrowly and shallowly incised. S₆ (Fig. 76): antecosta clearly curved medially, apodemal flexions moderately distant, apical process relatively short, L/W about 32/12, gradually tapering, lateral margins slightly outcurved, apex rounded. Genitalia (Figs. 87, 92, 98): Gonostylus arising from lateral side of gonocoxite, similar to *T. laeviceps*, basally 100 μ wide, gradually tapering (to 40 μ), subapically sinuate and slightly dilated (to 60 μ); apical part narrow, apex not dilated (33 μ wide). Penis valve horn like, distinctly shorter than gonostylus, 130 μ wide at base and 50 μ at middle; apically more distinctly sinuate and narrowed than in *T. laeviceps*, apical part rather distinctly curved, apex pointed.

Specimens examined: Holotype (Worker). Khao Chong-2, Peninsular Thailand. Paratypes. MALAYA Ulu Langat (1w), Gombak-c (1w), Kuala Lumpur-d (1w), Kuala Tranggan (1w), Kuala Tahan-a (1w), -b (8w), Taman Negara (16w), Kanching (1w), Penang-2 (2w), -4 (1w), -5a (1w), -5b (4w), Pasoh (12w); P. THAILAND Songkhla -c (1w), -d (2w), Khao Chong-2 (3w, 124♂).

This species was separated in the course of examination of Malayan specimens of *T. laeviceps* (cf. Fig. 106). Worker is similar to *T. pagdeni* by its small size and more or less banded mesoscutal hairs. But glabrous area G_3 is usually provided with sparse hairs so that band formation is less distinct than in *T. pagdeni*. Except size and mesoscutal bands, *T. pagdeniformis* is closely similar to *T. laeviceps* in various metric characters. Some deviations, e.g. in IOD/OOD, LOD/MOD, ML/FW, FL/FW, may be explained by allomorphic trends (Fig. 4). Distinction of *T. pagdeniformis* and small workers of *T. laeviceps* is sometimes very difficult and often impossible in the specimens of poor condition. I had thought this species as a dwarf form of *T. laeviceps*, until the discovery of males from Khao Chong, which showed subtle but stable differences in genitalia, in particular in the form of gonostylus.

As seen in Fig. 106 the specimens from Pasoh are larger than others:

	HW (mm)			WL ₂ (mm)		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
Pasoh	1.787	0.022	8	1.241	0.017	9
Other Malayan	1.711	0.034	27	1.132	0.056	30

Moreover, Pasoh workers differ from others by paler and sparser mesoscutal hairs (cf. Figs. 16~17). For the time being, these are identified with *T. pagdeniformis*, but closer studies are required on various populations in Malaya.

T. (T.) minor sp. nov.

The second smallest species of the subgenus and the smallest species of T. laeviceps group. Similar to T. pagdeniformis but distinguished by its smaller size, mesoscutal hairs admixed with more dark hairs, and narrower glabrous areas.

Worker: BL 3.2~3.4 mm, WL₁ 3.6~3.8 mm, HW ± 1.6 mm (Figs. 1, 2, Tab. 1), WL₂ ± 1.0 mm (Figs. 1, 3, Tab. 2), HTL ± 1.5 mm (Figs. 2, 3, Tab. 3). Blackish; antenna below testaceous; clypeus, tegula, legs and metasoma relatively dark (Tabs. 16~20), but in most specimens hind tibia posteriorly testaceous. Anterior veins and stigma deep brown. Frontal hairs whitish, not plumose (Tab. 22); mesoscutal hairs pale testaceous, with sparse but distinct admixture of darker hairs (Fig. 23), well banded but G_3 relatively narrow (Fig. 22); mesoscutellar fringe pale testaceous, with few admixture of dark bristles (Tab. 24); anterior corbicular bristles moderately dark (Tab. 25). WL₂/HW 0.70~0.75 (Figs. 1, 4, 6, Tab. 4), HTL/HW 0.95~1.05 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.45~1.55 (Figs. 3, 6, Tab. 6), EL/MOD 1.00~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.65~0.75 (Figs. 4, 6, Tab. 8), LOD/OOD 1.6~1.8 (Figs. 4, 6, Tab. 9), GW/EW 0.7~0.8 (Figs. 4, 6, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW small, 0.1~0.2 (Figs. 4, 6, Tab. 11), SC/EL small 0.50~0.55 (Tab. 12), FL/FW 0.7~0.8 (Figs. 4, 6, Tab. 13), HTW/HTL 0.32~0.36 (Figs. 5, 6, Tab. 14), HBW/HTW 0.5~0.6 (Fig. 6, Tab. 15).

Specimens examined: Holotype (Worker) and Paratypes (32 ww). Kuala Lumpur-2 (all from the same nest).

This species, described based upon a sample taken from the entrance of one and the same nest, is quite similar to *T. pagdeniformis*. After a little hesitation I gave it the specific rank by three features given in diagnosis. The relatively abundant admixture of dark hairs on mesoscutum is noteworthy, whereas pale testaceous longitudinal patch of hind tibia could be an artefact, as many specimens had once been preserved in alcohol.

T. (T.) gressitti sp. nov.

Worker characterized by distinctly melanic coloration including antenna below, and relatively long malar space. Male characterized by receded mandible, slender apical process of S_6 and apically clavate gonostylus.

Worker: BL 3.9~4.1 mm, WL_1 4.6~4.8 mm, HW 1.7~1.8 mm (Figs. 1, 2, Tab. 1), WL_2 1.2~1.3 mm (Figs. 1, 3, Tab. 2), HTL $\pm$ 1.6 mm (Figs. 2, 3, Tab. 3). Very melanic; body blackish to dark brown; scape and even alveolus blackish; flagella blackish, rarely with a slight chestnut tint; clypeus, tegula, legs and metasoma mostly dark brown to blackish (Tabs. 16~20). Anterior veins and stigma blackish brown. Frontal hairs, dark, not plumose (Tab. 22); mesoscutal hairs not well banded (Fig. 14), dark to blackish brown (Tab. 23); mesoscutellar fringe (Tab. 24) and anterior corbicular bristles (Tab. 25) dark. WL_2 /HW relatively large, 0.70~0.80 (Figs. 1, 4, 6, Tab. 4), HTL/HW small, 0.90~0.95 (Figs. 2, 4, 6, Tab. 5), HTL/ WL_2 small, 1.20~1.30 (Figs. 3, 6, Tab. 6), EL/MOD 0.95~1.05 (Fig. 6, Tab. 7), LOD/MOD 0.7~0.8 (Figs. 4, 6, Tab. 8), IOD/OOD 1.5~1.7 (Figs. 4, 6, Tab. 9), GW/EW 0.6~1.0 (Figs. 4, 6, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW relatively large 0.3~0.4 (Figs. 4, 6, Tab. 11), SC/EL large, 0.55~0.60 (Tab. 12), FL/FW 0.8~1.0 (Figs. 4, 6, Tab. 13), HTW/HTL 0.34~0.36 (Figs. 5, 6, Tab. 14), HBW/HTW 0.55~0.65 (Figs. 6, Tab. 15).

Male: WL_1 5 mm, HW 1.77 (Fig. 1, 2, Tab. 1), WL_2 1.4 mm (Fig. 1, 3, Tab. 2), HTL 1.75 mm (Figs. 2, 3, Tab. 3). Coloration as in worker but less melanic; scape below dirty testaceous, flagella below bright testaceous (Tab. 21). Frontal hairs not plumose (Tab. 22); erect occipital hairs long, 250 μ ; mesoscutal hairs testaceous, not well banded, relatively long, short hairs 100 μ , long hairs 175 μ ; mesoscutellar fringe and anterior hindtibial fringe testaceous (Tabs. 24, 25). Wing and hind tibia long relative to HW; WL_2 /HW 0.85 (Figs. 1, 7, Tab. 4), HTL/HW 1.00 (Figs. 2, 7, Tab. 5), HTL/ WL_2 1.35 (Figs. 3, 7, Tab. 6). Facial contour (Fig. 29) round, longer relative to width, vertex relatively raised; EL/MOD 1.10 (Tab. 7), LOD/MOD 0.7 (Fig. 7, Tab. 8), SC/EL 0.45 (Tab. 12), FL/FW 1.2 (Fig. 7, Tab. 13). Mandible receded (Fig. 107). Hair L of anterior and posterior margins of mid tibia and of posterior margin of mid basitarsus 175, 150, 175 μ ; posterior mid tibial fringe with poor admixture of plumose hairs (Fig. 34); mid basitarsus relatively long, L/L mid basitarsus/mid tibia 0.67. Hind tibia similar to

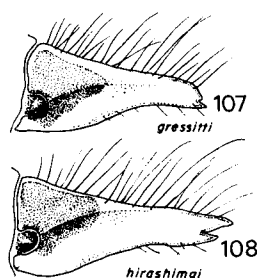
T. hirashimai (Figs. 5, 41) but HTW/HTL smaller 0.26~0.30 (Figs. 5, 7, Tab. 14), HBW/HTW 0.50~0.60 (Fig. 7, Tab. 15); outer surface flat, hairs homogenously dense and short, with no admixture of plumose ones both on surface and in posterior fringe (Figs. 41, 49, 55); hind basitarsus (Fig. 41) nearly parallel-sided; maximum hair L of posterior margin of hind tibia 150 μ , of hind basitarsus 125~150 μ ; W/L hind basitarsus small, 0.42.

Metasoma narrower than head. T_7 (Fig. 69) dorsapically not Y-ridged, apex broadly rounded. S_5 (Fig. 73): Antegladular area medially short, median depression of postgladular area very wide but not well demarcated, with very sparse hairs; apex narrowly but deeply emarginate. S_6 (Fig. 79): Antecosta rather straight, apodemal flexions widely distant; apical process very long and slender, L/W about 40/5, lateral margins basally convergent but in most part very gently tapering. Genitalia (Figs. 82A, B): Gonostylus arising from lateral side of gonocoxite; very long, 65 μ wide at base, gradually tapering, conspicuously sinuate at apical 1/3 (25 μ wide), apex clavate (75 μ wide). Penis valve rod like, slender, distinctly shorter than gonostylus, basally 85 μ and medially 80 μ wide, apical half forming a broad curve, apex not much pointed.

Specimens examined: Holotype (Worker). Fyan-b, Viet Nam. Paratypes. VIET NAM Fyan-a (1w, 1 δ), -b (48w), Dalat-1 (4w), -2 (1w), Balao-1b (1 δ , without head)

The species is dedicated to Dr. J.L. Gressitt, Bernice P. Bishop Museum, Honolulu.

Combination of workers and males is still tentative by the following two reasons: 1) Males are larger than workers (cf. Figs. 1, 2). 2) In workers antenna below is mostly blackish to dark brown, but in a male bright testaceous, just opposing to the tendency in other species, in which workers are pale but males often darker (cf. Tab. 21). On the other hand, general habitus, dark coloration and relatively long scape are common to both sexes. Although only two specimens were obtained, one of which was devoid of the head, males are remarkable by the features given in diagnosis, indicating a high specialization. Workers are also conspicuous by its melanism. In Tables 16~20, *T. gressitti* represents the most melanic tendencies. Moreover, antennal space and alveolus, being testaceous to ferruginous in all other species, are blackish. In size workers are comparable to the medium sized specimens of *T. laeviceps*, but easily distinguished by the dark coloration and differences in WL_2/HW , HTL/HW , HTL/WL_2 , and ML/FW . The difference in WL_2/HW is particularly clear when compared with the sympatric Vietnamese workers of *T. laeviceps* (cf. Fig. 105, F). The specimens from Fyan are generally more melanic than those from Dalat:



Figs. 107~108. Male left mandible of *T. gressitti* (receded) and *T. hirashimai* (normal).

Color degree	Scape		Flagella		Clypeus		Metasoma	
	Fyan	Dalat	Fyan	Dalat	Fyan	Dalat	Fyan	Dalat
IV		4		6		2		
V	41	2	41		20	4		6
VI					21		49	

T. (T.) iridipennis Smith

Trigona iridipennis Smith 1854. Catal. Hym. Brit. Mus. 2: 413.

Trigona praeterita Walker 1860. Ann. Mag. Nat. Hist. (3) 5: 305.

Trigona ruficornis Smith 1870 (nec Lamarek 1817). Tr. Zool. Soc. 7: 194; Dalla Torre 1896. Cat. Hym. 10: 583.

? *Trigona bengalensis* Cameron 1896. Mem. Proc. Manchest. Lit. Phil. Soc. 41: 143.

Melipona iridipennis, Bingham 1897: 563.

Melipona smithii Bingham 1897: 563.

Melipona praeterita, Bingham 1897: 564.

Meliponorytes devictus Cockerell 1921. Ann. Mag. Nat. Hist. (9)8: 544 (Fossil).

Trigona laeviceps, Cockerell (nec Smith) 1922. Nature: 714 (Fossil).

Trigona (Tetragona) iridipennis var. *iridipennis*, Schwarz 1939: 111 (partim).

Tetragonula iridipennis, Moure 1961: 208.

Trigona (Tetragona) iridipennis, Zeuner and Manning 1976: 222 (Fossil).

T. iridipennis is the type species of *Tetragonula* (Moure 1961), but Schwarz (1939) jointed *T. iridipennis* from India and Sri Lanka and *T. laeviceps* from S.E. Asia. Consequently *T. iridipennis* has been considered a species widespread from India to Solomon Islands (p. 201). Moure (1961) pointed out the size difference between two species but ignored more essential differences. Having examined many worker specimens from both areas, I have noticed clear differences between them in size, mesosomal hairs and some metric characters. Distinction became decisive when males from Sri Lanka, the type locality of *T. iridipennis*, were compared with those of *T. laeviceps* from S.E. Asia. Apparently two species represent each an independent group together with some allied ones, as defined in p. 234.

Distinction from the species of T. laeviceps group given in p. 234. Male easily distinguished from two other species of the same group by unusually dilated penis valve and very wide gonostylus, and workers from T. fuscobalteata by larger size, and from T. pagdeni by tegula, clypeus, legs and anterior corbicular bristles on the average darker.

Worker (Pl. V, Fig. 6): BL 3.6~3.9 mm, WL₁ 3.7~4.3 mm, HW 1.6~1.8 mm (Figs. 1, 2, Tab. 1), WL₂ 0.9~1.2 mm (Figs. 1, 3, Tab. 2), HTL 1.4~1.7 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below testaceous to ferruginous, occasionally dark brown; clypeus, tegula, legs and metasoma on the average relatively dark (Tabs. 16~20); metasoma not so frequently bicolorous as in *T. pagdeni*. Anterior veins and stigma dark brown. Frontal hairs fulvous to whitish, rarely brownish, often plumose (Tab. 22); mesoscutal hairs well banded (Figs. 20, 21), pale fulvous to testaceous, rarely darker (Tab. 23); mesoscutellar fringe fulvous to testaceous, occasionally with admixture of dark bristles (Tab. 24); anterior corbicular bristles variable, relatively pale to nearly blackish (Tab. 25).

WL₂/HW small, 0.60~0.70 (Figs. 1, 4, 6, Tab. 4), HTL/HW small 0.90~1.00 (Figs. 2, 4, 6 Tab. 5), HTL/WL₂ large, 1.35~1.60 (Figs. 3, 6, Tab. 6), EL/MOD 0.90~1.00 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.75 (Figs. 4, 6, Tab. 8), IOD/OOD large, 1.6~2.1 (Figs. 4, 6, Tab. 9), GW/EW 0.7~0.9 (Figs. 4, 6, Tab. 10), ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.2~0.3 (Figs. 4, 6, Tab. 11), SC/EL 0.50~0.55 (Tab. 12), FL/FW 0.7~0.9 (Figs. 4, 6, Tab. 13), HTW/HTL 0.32~0.40 (Figs. 5, 6, Tab. 14), HBW/HTW 0.50~0.60 (Fig. 6, Tab. 15).

Male: BL 3.8~4.0 mm, WL₁ 3.7~4.3 mm, HW 1.7~1.8 mm (Figs. 1, 2, Tab. 1), WL₂ 1.1~1.2 (Figs. 1, 3, Tab. 2), HTL 1.4~1.6 mm (Figs. 2, 3, Tab. 3). Coloration as in workers (Tabs. 16~20), but antenna below darker, chestnut to blackish brown, scape often blackish (Tab. 21). Frontal hairs mostly not plumose (Tab. 22); erect occipital hairs 150 μ ; mesoscutal hairs sparse, obscurely banded (Fig. 28), short hairs 75~100 μ , long hairs 125~150 μ ; mesoscutellar fringe pale, admixed bristles variable in color, fulvous to quite dark (Tab. 24); anterior hindtibial fringe dark brown to blackish (Tab. 25). WL₂/HW relatively small 0.65~0.75 (Figs. 1, 7, Tab. 4), HTL/HW relatively large 0.85~0.95 (Figs. 2, 7, Tab. 5), HTL/WL₂ large, 1.35~1.45 (Figs. 3, 7, Tab. 6). Facial contour (Fig. 30) intermediate between *T. hirashimai* (Fig. 31) and *gressitti* (Fig. 29), vertex medially rather raised. EL/MOD small, 1.05~1.15 (Tab. 7), LOD/MOD 0.60~0.70 (Fig. 7, Tab. 8), SC/EL 0.40~0.45 (Tab. 12), FL/FW small, 1.0~1.1 (Fig. 7, Tab. 13). Mandible normal (cf. Fig. 108). Hair L of anterior and posterior margins of mid tibia and of posterior margin of mid basitarsus 125 μ , posterior midtibial fringe with abundant admixture of plumose hairs (Fig. 38); L/L mid basitarsus/mid tibia 0.60. Hind tibia fairly wide (Figs. 5, 45), HTW/HTL 0.38~0.40 (Fig. 7, Tab. 14); outer surface posteriorly slightly convex, but not so as in *T. pagdeni*; hairs sparser antero-apically, with admixture of plumose hairs both on surface postapically and in posterior fringe (Figs. 45, 52, 59); hind basitarsus (Fig. 45) with posterior margin slightly divergent; maximum hair L of posterior margin of hind tibia 100~150 μ , of hind basitarsus 100 μ ; W/L hind basitarsus 0.52.

Metasoma narrower than head. T₇ (Fig. 65) dorsapically Y-ridged, lateral margins incurved, mildly angulate anteriorly, apex pointed. S₅ (Fig. 73): Antegladular area medially relatively long; postgladular area relatively short, median depression with sparse hairs, apex narrowly and shallowly incised. S₆ (Fig. 80): Antecosta conspicuously curved medially, apodemal flexions not widely distant; apical process short, L/W 30/11, lateral margins parallel-sided to gently incurved; apex rounded. Genitalia (Figs. 89, 91, 97): gonostylus arising from dorsum of gonocoxite, blade like, basally narrow (33 μ), gradually dilated (100 μ at middle), followed by tapering (to 20 μ); apical part lightly curved, apex rounded but not dilated. Penis valve blade like, unusually wide, 180 μ at middle where 25 μ thick, abruptly tapering and gently curved at apex.

Specimens examined: INDIA Dehra Dun (50w), Calcutta (4w), Nagpur (1w), Bombay-a (1w), -b (1w), -c (2w), Poona-a (50w), -b (11w), -c (1w), -d (1w), -e (1w), -f (1w), -g (1w), -h (1w), -i (3w), Lonavla (2w), Bangalore (4w), Madras-1 (26w), -2 (35w), -3a

(17w), -3b (1w), Kodaikanal (9w), Krum-Bagaram-a (2w), -b (1w), Pathanapuram (4w), Alwaye Khiaskam (1w); SRI LANKA Colombo-a (1w), -b (4w), -c (1w), Sigiriya (7w, 113♂), Nalando (1w), Uggalkaltota-a (4w), -b (2w), Wellawaya (2w), Kanneliya-a (7w), -b (1w), Kandy-1 (3w), -2 (1w), -3 (1w), -4 (2w), -5 (1w), Labugama (11w), Elephant Pass (3w), Palutapana (5w), Kottawa (2w), Hambatona (1w), Thwaites (1w), Sinharaja (1w), Trincomalee (1w), Lahugala-a (1w), -b (1w).

T. iridipennis redescribed here is very close to *T. pagdeni*. Workers of both species are nearly identical in size and metric characters (Figs. 1~6, Tabs. 1~15), though HTL/WL₂ and SC/EL are slightly different. Principal differences are relatively darker coloration and poor development of plumose hairs on frons in *T. iridipennis*, but both vary considerably among individuals. Some workers, e.g. from Nagpur, Bangalore, Madras, etc. are nearly identical with typical *T. pagdeni* in coloration.

HW and WL₂ of some samples represented by many specimens are presented in Table 28. Sinhalese specimens are on the average larger than Indian specimens. But a fairly large variation occurs within Sri Lanka (Table 29). In coloration Sinhalese workers are generally darker (Table 30), but there are some pale ones, too. Some workers from Colombo-d, Elephant Pass and Palutapana are particularly pale. These are mostly small. But there are also some small and dark specimens. It is premature to divide *T. iridipennis* in two forms, Sri Lanka (large and dark) and India (small and pale). Closer variation analyses by residential entomologists are expected.

Table 28. HW and WL₂ in some worker samples of *T. iridipennis* represented by many specimens (in mm)

	India				Sri Lanka	Total
	Dehra Dun	Poona	Madras and vicinity	Others combined		
HW						
$\bar{x}$	Shrunked by alcohol	1.652	1.679	1.703	1.744	1.693
SD		0.037	0.029	0.054	0.063	0.060
N		58	78	24	64	224
WL ₂						
$\bar{x}$	1.034	1.007	1.002	1.058	1.103	1.045
SD	0.033	0.033	0.027	0.040	0.058	0.048
N	47	59	63	28	61	249

Cockerell (1921, 1922) published two fossil records, *Meliponorytes devictus* and *Trigona laeviceps*, from Burmese amber, Hukong Valley. According to Zeuner and Manning (1976) both are probably from Pleistocene. The authors synonymized two fossils with *T. iridipennis*. Because *T. laeviceps* and *T. iridipennis* were now clearly distinguished, it must be asked whether these fossils are really *iridipennis* or not. Having visited the British Museum Dr. W.E. Kerr took some measurements with *M. devictus*, together with one specimen of

Table 29. Variation of worker HW of *T. iridipennis* in Sri Lanka

District (abbrev.)	N	Head width in micrometer scale (40=1 mm)														
		61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
COL	22							1	3	2	1		6	9		
MAT	10							2	1		1	1	4			1
RAT	7						1				1	2	2	1		
GAL	16					1	3		3	3		1	4	1		
KAN	8						1	1	2	2	1		1			
MON	2											1		1		
HAM	5							1	3					1		
AMP	2				1											1
TRI	1								1							
JEF	3				1			1	1							
Sri Lanka	76				2	1	5	6	14	7	4	5	17	13	1	1
India	162	1	1	5	6	13	43	38	31	15	5	2		2		

Table 30. Color variation in the Indian and Sinhalese populations of *T. iridipennis* (workers)

Areas	Metasomal integument						Frontal hairs						Frontal hairs plumosity			
	N	II	III	IV	V	VI	N	white	pale	fulvous	dark	N	+	±	-	
India	205	3	11	82	84	25	149	86	63			156	97	58	1	
Sri Lanka	64			4	25	35	62	5	30	15	12	63		33	30	

Areas	Mesoscutal hairs						Mesoscutellar bristles						Anterior corbicular fringe						
	N	II	III	IV	V	VI	N	I	II	III	IV	V	N	I	II	III	IV	V	VI
India	120	67	27	14	12		205	15	160	21	8	1	210	2	95	85	14	14	
Sri Lanka	63	7	10	26	12	8	62		6	6	40	10	67		3	6	4	36	18

"*T. iridipennis*" (British Museum, No. 2-94, Bingham Coll. 96-3 from Tenasserim). Fortunately, I could examine the latter specimen by the courtesy of Dr. G.R. Else and identified it with *T. pagdeni*. The synoptic table by Kerr (in Kerr and Maule 1964) shows that *M. devictus* is clearly smaller than the specimen from Tenasserim, e.g. HW 1.35 mm against 1.55 mm and HTL 0.925 mm against 1.475 mm. Therefore, it is likely that the fossil is either *T. iridipennis* or *pagdeni*, or possibly *T. fuscobalteata* (cf. Tabs. 1, 2), not *T. laeviceps*.

T. (T.) pagdeni Schwarz

Trigona (Tetragona) fuscobalteata var. *pagdeni* Schwarz 1939: 110; 1951: 63; Sakagami and Yoshikawa 1961: 24.

Tetragonula pagdeni, Moure 1961, 208.

This form was originally described as a variety of *T. fuscobalteata*, based upon two males from Nakon Sri Tamarat, Thailand, and some workers from the same locality and Singora (=Songkhla). The males were structurally close to *T. fuscobalteata* but larger. *T. pagdeni* and *T. fuscobalteata* are certainly very similar. But they are easily distinguished by size (cf. Figs. 1~3) and differ in some subtle features given in p. 225. Moreover, they are partially sympatric. Therefore, two forms are considered here independent species. Schwarz mentioned that *T. pagdeni* workers were as large as *T. iridipennis* (=smaller specimens of *T. laeviceps* in the present paper), but differed in three features:

	<i>laeviceps</i>	<i>pagdeni</i>
Anterior corbicular fringe	black	silvery gray
Mesoscutal hairs	not banded	banded
Metasoma and legs	darker	paler.

These differences are essentially valid. On the other hand, *T. pagdeni* and real *T. iridipennis* redefined in p. 216 are very similar for each other, in worker distinguished only statistically.

Distinction from species of laeviceps group given in p. 201 and 234. Male easily distinguished from T. iridipennis by narrower gonostylus and penis valve, whereas worker only statistically, mainly by paler coloration, in particular, of anterior corbicular fringe, and by more plumose frontal hairs. Structurally nearly identical with T. fuscobalteata but much larger both in worker and male.

Worker (Pl. V, Fig. 7): BL 3.4~3.9 mm, WL₁ 3.9~4.1 mm, HW 1.6~1.8 mm (Figs. 1, 2, Tab. 1), WL₂ 1.0~1.2 mm (Figs. 1, 3, Tab. 2), HTL 1.4~1.7 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below testaceous to ferruginous; clypeus, tegula and legs relatively pale (Tabs. 16~19); metasoma apically dark to blackish brown (Tab. 20), basally predominantly paler, testaceous to pale brown, showing bicolorism. Anterior veins and stigma testaceous to deep brown. Frontal hairs mainly whitish and distinctly plumose (Tab. 22); mesoscutal and mesoscutellar hairs pale fulvous, admixture of dark hairs rare (Tabs. 23, 24); mesoscutal hairs distinctly banded (Fig. 19); anterior corbicular bristles principally pale (Tab. 25). WL₂/HW small, 0.65~0.70 (Figs. 1, 4, 6, Tab. 4), HTL/HW small, 0.90~0.95 (Figs. 2, 4, 6, Tab. 5), HTL/WL₂ 1.35~1.50 (Figs. 3, 6, Tab. 6), EL/MOD 0.90~1.00 (Fig. 6, Tab. 7), LOD/MOD 0.70~0.75 (Figs. 4, 6, Tab. 8), IOD/OOD large, 1.6~1.9 (Figs. 4, 6, Tab. 9), GW/EW 0.6~0.9 (Figs. 4, 6, Tab. 10), ocellocapital distance about 1/2 of ocellar diameter (cf. Fig. 104), ML/FW 0.2~0.3 (Figs. 4, 6, Tab. 11), SC/EL 0.50~0.60 (Tab. 12), FL/FW 0.7~0.9 (Figs. 4, 6, Tab. 13), HTW/HTL 0.34~0.40 (Figs. 5, 6, Tab. 14), HBW/HTW 0.50~0.55 (Fig. 6, Tab. 15).

Male BL 3.6~3.8 mm, WL₁ 3.8~4.0 mm, HW 1.6~1.7 mm (Figs. 1, 2, Tab. 1), WL₂ 1.0~1.1 mm (Figs. 1, 3, Tab. 2), HTL 1.4~1.5 mm (Figs. 2, 3, Tab. 3). Coloration as in worker; antenna below testaceous to deep brown (Table 21).

Frontal hairs usually more or less plumose (Tab. 22); erect occipital hairs $150\ \mu$; mesoscutal hairs sparse, obscurely banded (Fig. 26), short hairs $100\ \mu$, long hairs $125\ \mu$; mesoscutellar fringe pale, dark bristles few if any (Tab. 24). WL_2/HW small, $0.65\sim 0.75$ (Fig. 1, Tab. 4), HTL/HW large $0.90\sim 0.95$ (Fig. 2, Tab. 5), HTL/WL_2 large, $1.30\sim 1.40$ (Fig. 3, Tab. 6). Facial contour as in *T. iridipennis* (cf. Fig. 30), vertex medially rather raised; EL/MOD small, $0.90\sim 1.00$ (Tab. 7), LOD/MOD $0.65\sim 0.70$ (Fig. 7, Tab. 8), SC/EL $0.40\sim 0.45$ (Tab. 12), FL/FW small, $1.0\sim 1.1$ (Fig. 7, Tab. 13). Mandible normal (cf. Fig. 108). Hair L of anterior and posterior margins of mid tibia and of posterior margin of mid basitarsus $125\ \mu$; posterior midtibial fringe with abundant admixture of plumose hairs (Fig. 37); L/L mid basitarsus/mid tibia 0.62 . Hind tibia fairly wide (Figs. 5, 46), HTW/HTL 0.40 or more (Fig. 7, Tab. 14); outer surface posteriorly mildly convex, much than in *T. iridipennis*; posterior hairs sparser and admixture of plumose hairs more abundant than in *T. iridipennis*; posterior fringe also with rich long plumose hairs (Figs. 46, 5, 60); hind basitarsus (Fig. 46) with posterior margin rather divergent and gently outcurved; maximum hair L of posterior margin of hind tibia $175\ \mu$, of hind basitarsus $125\ \mu$; W/L hind basitarsus 0.55 .

Metasoma narrower than head. T_7 (Fig. 66) dorsapically Y-ridged; apex less pointed than in *T. iridipennis*, apical lateral margin rather straight, anteriorly less angulate than in *T. iridipennis*. S_5 as in *T. iridipennis*. (cf. Fig. 73). S_6 (Fig. 81): Antecosta distinctly curved; distance between apodemal flexions short; apical process very short, L/W only $2/1$, lateral margins subparallel to gently convergent, apex rounded. Genitalia (Figs. 88, 90, 96): Gonostylus arising from dorsum of gonocoxite, blade like, but distinctly narrower than in *T. iridipennis*, basally $33\ \mu$, medially $50\ \mu$ and apically tapering to $15\sim 20\ \mu$ wide; apex rounded but not dilated. Penis valve rod like, basally $125\ \mu$ wide, seen laterally thicker than in *T. iridipennis*, gradually tapering; apex mildly pointed.

Specimens examined: P. THAILAND Banna (8w), Satun (3w), Songkhla-a (1w), -c (13w), -d (1w), Nacon Sritamaraj-a (2w), -b (1w), Kor Hong (53♂); S. THAILAND Chantaburi/Prew-b (39♂), -c (132w), -d (17w), -e (21w), -f (3w), -g (2w), -h (3w), -i (10w from a nest), -j (5w), Khanchanaburi (1w), Skiracha (3w), Choburi (5w), Bangkok-a (32w), -b (1w), -c (8w), -d (2w), -e (5w), -f (7w), -g (6w), -h (15w), -i (1w), -j (6w), -k (20w), Korat (1w), Kamphangpet (1w); E. THAILAND Kamacha Eé (13w), Mukadaharn (16w), Ubol (1w); N. THAILAND Uthaitani (73w), Jam Ngow Tak (2w), Chiang Mai-1a (1w), -1b (23w), -1c (14w), 1d (18w), -1e (3w), -1f (1w), -2 (1w), Chiang Dao-a (44w), -d (1w), Muang Fang-1 (1w), Mae Fack-1 (1w), Doi Dao (1w), Fang-1a (15w), -1b (6w), -2b (2w); CAMBODIA Oudong (1w), Kon Pom Cham (1w); VIET NAM Phan Thiet (1w); LAOS Pakse (1w); TENASSERIM Maul Maia (1w).

According to Schwarz (1939) his two males possessed scape below black and flagella below ferruginous. Cockerell (1929) recorded males of *T. sapiens* with black scape from Gaudalcanal Island. Schwarz also examined a single male with ferruginous scape from Solomon Islands. The accompanied workers were scarcely separable from his *T. iridipennis*. From these information, he assumed the

occurrence of both *iridipennis* (= *sapiens*, = *laeviceps* in the present paper) and *fuscobalteata pagdeni* in Solomon Islands. Scape of my male specimens varied from deep testaceous to dark brown but did not attain black (degree VI, cf. Tab. 21). From the correspondence of other character features, it is hardly possible that Schwarz and I dealt with two different species in Thailand. Possibly coloration of scape is somewhat variable as suggested in Table 21, particularly in *T. fuscobalteata*. Through the courtesy of Dr. G.R. Else, British Museum, I could examine a single worker labelled "Solomon Is., Rendova Kokorana, 1-14-1954, E.S. Brown, *Trigona iridipennis* Sm. det by Karl V. Krombein 1957" (cf. Fig. 105, B, V₄). The specimen was apparently *T. laeviceps* defined in the present paper, not *T. pagdeni*, though wings were relatively short. It must also be mentioned that *T. pagdeni* is one of the commonest species in Thailand but so far not recorded from Malaya.

Color variation of some body parts are given in Table 31. As in Table 20 metasomal color was classified according to darker apical terga, ignoring bicolorism very frequent in this species. According to Schwarz, anterior corbicular fringe is mainly silvery gray. In my specimens, this palest degree appeared only sporadically. Note the occurrence of very dark corbicular bristles in some workers.

Table 31. Color variation of *T. pagdeni* workers in various areas

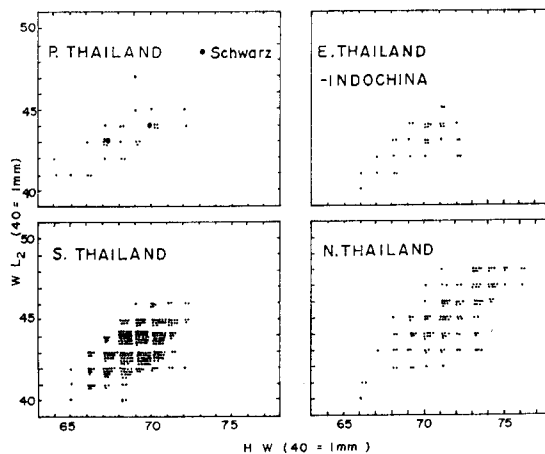
Areas	Clypeus					Tegula				Fore trochanter				Hind tibia				
	N	III	IV	V	VI	N	III	IV	V	N	II	III	IV	N	III	IV	V	VI
Peninsular Thailand	21		6	13	2	29	7	15	7	29		24	5	32	1	21	10	
E. Thailand + Cambodia	31		14	17		31	2	22	7	30		24	6	32		4	18	10
S. Thailand	241	15	136	83	7	258	62	167	29	251	38	200	13	267	12	154	98	3
N. Thailand	143	4	59	79	1	166	29	96	41	162	6	125	31	200	8	77	101	14
Viet Nam	10			10		5	4	1		5	1	4		6	2	1	3	
+ Laos																		
Tenasserim	1			1		1		1		1		1		1		1		

Areas	Metasoma						Mesoscutal hairs					Mesoscutellar bristles					Anterior corbicular fringe							
	N	II	III	IV	V	VI	N	II	III	IV	V	N	I	II	III	IV	V	N	I	II	III	IV	V	VI
Peninsular Thailand	31		2	13	11	5	19	10	7	2		32	9	10	10	3		62	3	44	15			
E. Thailand + Cambodia	30			6	11	13	19	18	1			31		28	3			31		27	3			1
S. Thailand	280	4	12	119	114	31	87	67	15	1	4	265		190	57	14	4	268	1	181	71	12	3	
N. Thailand	197		19	77	76	25	112	96	15	1		189	29	91	51	18		177	14	57	76	28	2	
Viet Nam	4		2	2			3	2	1			5		5				5	4				1	
+ Laos																								
Tenasserim	1			1			1		1			1			1			1			1			

Some male specimens from Chantaburi were conspicuous by metasoma, clypeus and scape very dark, especially apical terga frequently jet black. In general, however, no clear regional gradient in coloration was recognized. A single worker from Tenasserim was tentatively identified with *T. pagdeni*, as its coloration was just as pale as average specimens from Thailand, and frons was provided with whitish plumose hairs. But the actual boundary of two allopatric species, *T. iridipennis* and *pagdeni*, may be solved only by examination of a good number of Burmese specimens, especially of males.

T. pagdeni increases the size northward (Fig. 109, Tab. 32). The samples from N. Thailand involve some fairly large workers. The same tendency is suggested in males obtained from two different localities:

Locality	HW		N	WL ₂		N
	$\bar{x}$	SD		$\bar{x}$	SD	
Kor Hong, P. Thailand	1.666	0.034	54	1.104	0.030	52
Chantaburi, S. Thailand	1.698	0.036	28	1.111	0.017	26



Figs. 109. WL_2/HW relation in *T. pagdeni* workers in four areas. Schwarz=workers identified with *T. pagdeni* by H.F. Schwarz.

T. (T.) fuscobalteata Cameron

Trigona fuscobalteata Cameron 1908. Entomologist 41: 192; Schwarz 1937: 310.

Trigona pallidistigma Cameron 1908. Entomologist 41: 192.

Trigona atomella Cockerell 1919. Ann. Mag. Nat. Hist. (3)9: 243; 1920: (5)9: 116; 1929: (4)10: 590; Schwarz 1937: 311.

Trigona pygmaea Friese 1933. Naturh. Maandbl. 22: 147.

Trigona (Tetragona) fuscobalteata var. *fuscobalteata*, Schwarz 1939: 107;

Tetragonula fuscobalteata, Moure 1961: 209.

Table 32. HW, WL₂ and HTL of *T. pagdeni* workers in various areas (in mm)

Areas	HW	WL ₂	HTL
N. Thailand			
$\bar{x}$	1.779	1.127	1.566
SD	0.052	0.049	0.053
N	181	166	45
S. Thailand			
$\bar{x}$	1.715	1.087	1.553
SD	0.033	0.029	0.040
N	248	278	128
Pen. Thailand			
$\bar{x}$	1.693	1.077	1.539
SD	0.053	0.037	0.026
N	28	28	19
Others combined			
$\bar{x}$	1.748	1.080	1.522
SD	0.042	0.030	0.044
N	36	32	29

Tetragonula pallidistigma, Moure 1961: 209.

Trigona (*Tetragona*) *fuscobalteata fuscobalteata*, Yoshikawa, Ohgushi and Sakagami 1969: 173.

According to Schwarz (1939), *T. fuscobalteata* was named by the callow stage and *T. atomella* by the more fully colored adult of the same species. Moure (1961) mentioned that the type specimen of *T. atomella* from Penang was a little larger than that of *T. fuscobalteata* from Medang, Sarawak, WL₁ 3.3 mm, HW 1.36 mm against 3.1 and 1.35 mm respectively. The variation range given in Fig. 1 and Tabs. 1, 2 suggests both are conspecific. According to Moure (1961), *T. pallidistigma* is the callow of *T. fuscobalteata*.

The smallest species of the subgenus. Closely similar to T. pagdeni in coloration, pilosity, proportions and male structures, but distinctly smaller and male gonostylus a little dilated subapically. Distinction from T. minor, the next small species, is easy by more plumose frontal hairs, paler mesoscutal hairs, paler anterior corbicular bristles, smaller WL₂/HW, HTL/HW and larger IOD/OOD.

Worker (Pl. V, Fig. 5): BL 2.8~3.2 mm, WL₁ 3.1~3.4 mm, HW 1.35~1.5 mm (Figs. 1, 2, Tab. 1), WL₂ 0.9~1.0 mm (Figs. 1, 3, Tab. 2), HTL 1.2~1.4 mm (Figs. 2, 3, Tab. 3). Black to blackish brown; antenna below testaceous to ferruginous, occasionally darker; clypeus paler or not (Tab. 16); tegula, legs and metasoma relatively pale (Tabs. 17~20); metasoma frequently paler basally, tending to bicolorism. Anterior veins and stigma testaceous to deep brown, occasionally dark brown. Frontal hairs mainly whitish and frequently plumose (Tab. 22); mesoscutal and mesoscutellar hairs pale fulvous, virtually without

admixture of dark bristles (Tabs. 23, 24), mesoscutal hairs well banded (Fig. 23); anterior corbicular bristles pale (Tab. 25). WL_2/HW small, $0.65\sim 0.75$ (Figs. 1, 4, 6, Tab. 4), HTL/HW small, $0.90\sim 1.00$ (Figs. 2, 4, 6, Tab. 5), HTL/WL_2 $1.35\sim 1.55$ (Figs. 3, 6, Tab. 6), EL/MOD $0.95\sim 1.05$ (Fig. 6, Tab. 7), LOD/MOD small, $0.65\sim 0.75$ (Figs. 4, 6, Tab. 8), IOD/OD large, $1.7\sim 2.1$ (Figs. 4, 6, Tab. 9), GW/EW $0.6\sim 0.8$ (Figs. 4, 6, Tab. 10), ocellocipital distance about $1/2$ of ocellar diameter (cf. Fig. 104); ML/FW $0.2\sim 0.3$ (Figs. 4, 6, Tab. 11), SC/EL $0.50\sim 0.55$ (Tab. 12), FL/FW $0.8\sim 1.0$ (Figs. 4, 6, Tab. 13), HTW/HTL $0.32\sim 0.36$ (Figs. 5, 6, Tab. 14), HBW/HTW $0.50\sim 0.55$ (Fig. 6, Tab. 15).

Male: BL $2.9\sim 3.0$ mm, $WL_1 \pm 3.4$ mm, HW $1.35\sim 1.45$ mm (Figs. 1, 2, Tab. 1), WL_2 $0.9\sim 1.0$ mm (Figs. 1, 3, Tab. 2), HTL $1.2\sim 1.4$ mm (Figs. 2, 3, Tab. 3). Coloration generally as in worker, though examined specimens being darker in clypeus, tegula, legs and metasoma (Tabs. 16~20); antenna below mostly dark to blackish brown (Tab. 21). Frontal hairs often more or less plumose; erect occipital hairs $100\sim 125\ \mu$; mesoscutal hairs sparse, obscurely banded, short hairs $50\ \mu$, long hairs $100\sim 125\ \mu$; mesoscutellar fringe pale, virtually without admixture of dark bristles (Tab. 24); anterior hindtibial fringe very pale (Tab. 25). WL_2/HW $0.70\sim 0.75$ (Fig. 1, Tab. 4), HTL/HW large, $0.90\sim 0.95$ (Figs. 2, Tab. 5), HTL/WL_2 large, $1.25\sim 1.40$ (Fig. 3, Tab. 6). Facial contour as in *T. iridipennis* (cf. Fig. 30), vertex medially rather raised; EL/MOD larger than in *T. iridipennis* and *pagdeni* $1.05\sim 1.15$ (Tab. 7); LOD/MOD small, $0.60\sim 0.70$ (Fig. 7, Tab. 8); SC/EL $0.40\sim 0.45$ (Tab. 12), FL/FW small, $1.0\sim 1.1$ (Fig. 7, Tab. 13). Mandible normal (cf. Fig. 108). Hair L of anterior and posterior margins of hind tibia and of posterior margin of mid basitarsus $100, 100, 100\sim 125\ \mu$; posterior midtibial fringe with abundant admixture of plumose hairs though slightly less than in *T. pagdeni* (Fig. 39), L/L mid basitarsus/mid tibia 0.65 . Hind tibia fairly wide (Figs. 5, 47), HTW/HTL $0.32\sim 0.38$ (Fig. 7, Tab. 14); outer surface posteriorly mildly convex as in *T. pagdeni*; hairs as in *T. pagdeni*; posterior fringe also with rich long plumose hairs (Figs. 47, 53, 61); hind basitarsus (Fig. 47) with posterior margin not so divergent as in *T. pagdeni*; maximum hair L of posterior margin of hind tibia $150\ \mu$, of hind basitarsus $100\ \mu$; W/L hind basitarsus 0.50 .

Metasoma narrower than head. T_7 , and S_5 as in *T. pagdeni* (cf. Figs. 66, 73). S_6 (Fig. 75) as in *T. pagdeni*, lateral margins of apical process slightly to rather distinctly convergent, L/W $13/8$. Genitalia as in *T. pagdeni* (Fig. 88), except for gonostylus subapically slightly dilated ($30\ \mu$), otherwise width $25\ \mu$ from base to middle and $12\ \mu$ at apex (Fig. 95 vs. 96).

Specimens examined: MALAYA Subang (3w), Kuala Tranggan (1w), Taman Negara (9w), Fenting Sempak (34w, 56♂), Tapah (9ww from a nest), Gombak-d (9w), -e (59w), Kuala Lumpur-3b (2w), Penang-5b (13w); P. THAILAND Banna (40w), Yala (1w); S. THAILAND Chantaburi-a (5w), -d (13w), -f (1w); N. THAILAND Chiang Dao -d (13w), -f (1w).

This species is just a miniature copy of *T. pagdeni* except some slight differences: Worker. WL_2/HW , HTL/HW , FL/FW , EL/MOD larger while $HTW/$

HTL smaller. Male. EL/MOD larger, HTW/HTL smaller, scape below darker, mid tibia posteriorly with less admixture of plumose hairs, gonostylus wider subapically. Except male scape and gonostylus, the differences are so subtle that appreciable only by examining many specimens. Interestingly WL_2/HW , HTL/HW and FL/FW behave somewhat against the allomorphic trends in the subgenus (Fig. 4). Fig. 110 presents WL_2/HW relation in some worker samples. The sample from Taman Negara is quite heterogenous, involving some large workers nearly attaining the size of *T. minor*. Within the samples examined, no clear size gradient as in *T. pagdeni* is detected.

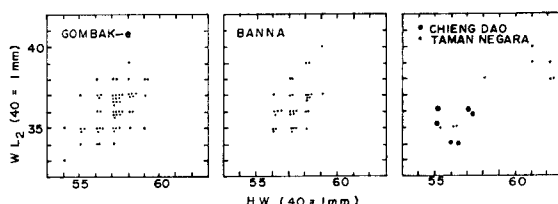
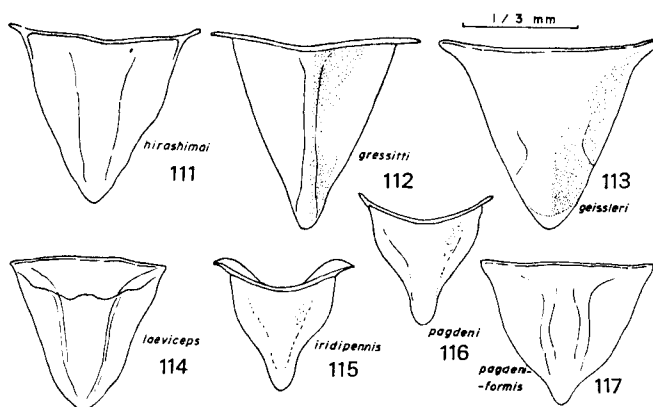


Fig. 110. WL_2/HW relation in *T. fuscobalteata* workers in four localities.



Figs. 111~117. Male sternum VI (S_6) of seven *Tetragonula* species.

Key to the Continental *Tetragonula* species

Workers

As repeated in the preceding pages, workers of some species can be distinguished only statistically. These cases are shown below with asterisks.

1. Concolorously honey testaceous. Relatively large, BL 5 mm, WL 4.7~5 mm, HW ± 2.1 mm *melina*

- At least head excluding clypeus and mesosoma dark brown to black..... 2
- 2. Very large (Figs. 1~3), BL more than 5.3 mm, WL₁ more than 5.8 mm. Gena wide (Fig. 101), GW/EW 1.0 or more (Tab. 10), ocelloccipital distance nearly as wide as ocellar diameter (Fig. 103)*latigenalis* nov.
- Gena narrower (cf. Fig. 102), GW/EW less than 1.0, ocelloccipital distance about 1/2 of ocellar diameter (cf. Fig. 103) 3
- 3. Very small (Figs. 1~3), BL and WL₁ less than 3.9 mm, HW 1.5 mm or less. Mesoscutal hairs sparse and well banded (Fig. 23)*fuscobalteata*
- Larger. BL more than 3.2 mm, HW 1.6 mm or more. In subtle case (*minor* nov.) mesoscutal hairs darker 4
- 4. Antenna below including alveolus blackish brown to black, rarely dark brown*gressitti* nov.
- Antenna below testaceous to ferruginous, only exceptionally dark brown .. 5
- *5. Mesoscutal hairs more or less well banded (Figs. 15~23), at least G₃ (Fig. 23) detectable 6
- *- Mesoscutal hairs not well banded (Figs. 8~14), G₃ indistinct..... 10
- 6. Large species, BL more than 4.7 mm, WL more than 4.9 mm, HW more than 2.1 mm*hirashimai* nov.
- Small species, BL less than 4.1 mm, WL₁ less than 4.5 mm, HW less than 1.8 mm 7
- *7. Small species, BL less than 3.4 mm, WL₁ less than 3.8 mm, HW about 1.6 mm. Mesoscutal hairs sparse but with distinct admixture of dark bristles and bands wider (Fig. 22). WL₂/HW 0.65~0.75, HTL/HW 0.95~1.05
.....*minor* nov.
- *- Larger, BL mostly more than 3.4 mm, WL₁ more than 3.7 mm, HW more than 1.6 mm. Mesoscutal hairs sparser, with fewer admixture of dark bristles 8
- *8. WL₂/HW 0.70~0.75 (Tab. 4), HTL/HW 0.95~1.05 (Tab. 5), EL/MOD 1.00~1.05 (Tab. 7) (Malaya and Peninsular Thailand)*pagdeniformis* nov.
- *- WL₂/HW 0.60~0.70 (Tab. 4), HTL/HW 0.85~1.00 (Tab. 5), EL/MOD 0.90~1.00 (Tab. 7) 9
- *9. Metasoma, legs and anterior corbicular fringe darker. Frontal hairs relatively dark and less plumose (Tabs. 18~20, 22) (India and Sri Lanka) ..*iridipennis*
- *- Metasoma, legs and anterior corbicular fringe paler. Frontal hairs mainly whitish and distinctly plumose (Tabs. 18~20, 22) (Thailand and Indochina)
.....*pagdeni*
- 10. Large species with long hind tibia, HTL more than 2 mm (Tab. 3), HTL/HW 1.05~1.10. Anterior veins and stigma testaceous to deep brown
.....*geissleri*
- Smaller with HTL less than 2 mm (Tab. 3) and HTL/HW 0.95~1.05 (Tab. 5)
..... 11
- *11. Larger, BL 4.4 mm or more, WL₁ 4.9 mm or more, HW 2.0 mm or more (Tab. 1). Anterior veins and stigma dark to blackish brown. Mesoscutal

- hairs mainly dark (Tab. 23) *zucchi* nov.
- *- Smaller, usually BL less than 4.6 mm, WL₁ less than 4.8 mm, HW less than 2.0 mm (Tab. 1). Mesoscutal hairs principally pale with admixture of some dark hairs (Tab. 23) 12
12. Dark species, metasoma mainly dark to blackish brown (Tab. 20). Clypeus, tegula and legs principally dark (Tabs. 16~19). Anterior veins and stigma dark to blackish brown *laeviceps*
- Paler species, metasoma ferruginous to chestnut brown (Tab. 20). Clypeus, tegula and legs pale (Tabs. 16~19). Anterior veins and stigma pale brown *sarawakensis*

Males

1. Gonostylus arising from dorsum of gonocoxite, penis valve blade like (Figs. 88~89). T₇ dorsapically Y-ridged (Figs. 65, 66). Hairs on hind tibia partly sparse and plumose, posterior fringe with rich plumose hairs (Figs. 45~47, 51~53, 59~61). Small species, BL less than 4.0 mm, HW less than 1.7 mm (Tab. 1) *iridipennis* group 2
- Gonostylus arising from side of gonocoxite, penis valve horn or rod like (Figs. 82, 83, 85~87) 4
2. Both penis valve and gonostylus very wide (Fig. 89), maximum width 180 and 100 μ respectively *iridipennis*
- Both penis valve and gonostylus narrower (Fig. 88), maximum width (in *pagdeni*) 125 and 50 μ respectively 3
3. Larger, BL 3.6~3.8 mm, WL₁ 3.8~4.0 mm, HW 1.6~1.7 mm (Tab. 1). Antenna below testaceous to deep brown (Tab. 21). Gonostylus subapically slender (Fig. 96) *pagdeni*
- Smaller, BL 2.9~3.0 mm, WL₁ $\pm$ 3.4 mm, HW 1.35~1.45 mm (Tab. 1). Antenna below dark to blackish brown (Tab. 21). Gonostylus subapically slightly dilated (Fig. 95) *fuscobalteata*
4. Mandible receded (Fig. 107). Gonostylus much longer than penis valve, apically conspicuously clavate (Fig. 82). Hind tibia narrow, hairs homogenously dense, short and not plumose (Fig. 41), posterior fringe without plumose hairs (Figs. 41, 49, 55) *gressitti* nov.
- Mandible normal (cf. Fig. 108). Gonostylus apically not clavate (Figs. 83, 85~87) 5
5. Metasoma wider than head. Gonostylus very slender ($\pm$ 25 μ) with subapical dilation (50 μ). Penis valve very robust (Fig. 85). Hind tibia with some plumose hairs on surface postapically and in posterior fringe (Figs. 43, 50, 57) *geissleri*
- Metasoma narrower than head. Gonostylus moderately wide. Penis valve less robust (Figs. 83, 86, 87). Hind tibia without plumose hairs (Figs. 40, 42, 44, 48, 54, 56, 58) *laeviceps* group 6

6. Large species, BL 5.3~5.5 mm, WL₁ 4.8~5.2 mm, HW 2.1~2.2 mm (Tab. 1). Antegladular area of S₅ medially short (Fig. 70). Gonostylus subapically distinctly dilated (Fig. 83) *hirashimai* nov.
- Smaller, BL less than 5.0 mm, WL₁ less than 4.7 mm, HW less than 1.8 mm (Tab. 1). Antegladular area of S₅ relatively long (cf. Fig. 73). Gonostylus subapically not or only slightly dilated (Figs. 84, 98~99) 7
7. Relatively large, BL 4.1~4.8 mm, WL₁ 4.4~4.7 mm. Gonostylus subapically not dilated (Fig. 99) *laeviceps*
- Relatively small, BL 4.0~4.4 mm, WL₁ 4.2~4.4 mm. Gonostylus subapically slightly dilated (Fig. 98) *pagdeniformis* nov.

Formae incertae sedis

Beside the species described and recorded above, there are some worker specimens of *Tetragonula* at my disposal, which slightly differ from some of the species described but cannot be identified accurately. These are mentioned here with alphabetic codes. The size of these forms is given in Figs. 1~3.

Forma TK: LAOS Thakhek-b (1w); VIET NAM Pleiku-1 (1w). Both are involved within the size range of *T. hirashimai* m. and frontal hairs are relatively plumose, especially in the Thakhek worker. Mesosomal hairs are also relatively pale as in *T. hirashimai*. But admixture of dark bristles in mesoscutellar fringe is richer and mesoscutal hairs are not so well banded. Two specimens are thus intermediate between *T. hirashimai* and large specimens of *T. laeviceps*. These might represent eastern populations of *T. hirashimai*, but their status cannot be solved until more materials are examined.

Forma UB: LAOS Thakhek-a (1w); E. THAILAND Ubol (3w). As given in Figs. 1~3, these workers are comparable to *T. laeviceps* in size, but mesoscutal hairs are sparser and obscurely banded as in *T. pagdeniformis* (less conspicuously in one Ubol specimen). These might represent a northern form of *T. pagdeniformis*, being larger in size. Even if this is the case, however, these workers should not be conspecific with two males of *T. laeviceps* obtained in Ubol on the same date, as their gonostylus was of the type of *laeviceps*, not of *pagdeniformis* (cf. Figs. 98 vs. 99). Or, *T. laeviceps* might produce some specimens with more or less banded mesosomal hairs. In such case distinction of *T. pagdeniformis* and the banded form of *T. laeviceps* may become somewhat similar to that of *T. zucchini* and the northern, large-sized *T. laeviceps* (cf. *T. zucchini*, p. 209).

Forma BG: INDIA Bangalore (2w). Two workers were collected together with four workers of *T. iridipennis*. The coloration is similar to *T. sarawakensis* but both are much larger and HW and WL₂ are large relative to HTL (Figs. 1~3). *Certainly these workers indicate the occurrence of a second Tetragonula species in India.*

Forma BGA: Andaman Is. (1w). Coloration is intermediate between *T.*

sarawakensis or forma BG and pale specimens of *T. laeviceps*, but paler parts not so distinctly patched as in *T. sarawakensis* or forma BG. Size is comparable to a large *T. laeviceps* worker, eyes are crushed but HTL/WL₂ is opposite to BG (Fig. 3). Possibly this represents an insular form or vicariant of *T. laeviceps*.

Systematic considerations

The subgenus *Tetragonula* is the largest and most widespread group in the Indopacific stingless bees. The present paper only deals with the continental species. Moreover, males provided with more reliable diagnostic characters are known only in eight out of 13 species. The following considerations are, therefore, inevitably of preliminary nature.

Among the Indopacific stingless bee groups, *Tetragonula* is certainly closest to *Tetragonilla*,¹⁾ sharing a specialized (apomorphic) character state, emphatically projected mesoscutellum exceeding propodeum. That this coincidence indicates the common descent than a parallelism is favored by many other features common to both subgenera (cf. Moure 1961). Among the differences in workers between both subgenera, Moure stressed the following features (p. 189 and 211).

Character	<i>Tetragonula</i>	<i>Tetragonilla</i>
1a) Face	narrower than eye length	almost as wide as eye length
1b) Upper alveolar tangent	well below mid-face	a little below mid-face
1c) Inter-alveolar distance	half of alveorbital distance	more than half of alveorbital distance
2a) Scape	conspicuously shorter than alveocellar distance, ending well below lower tangent of median ocellus	about as long as alveocellar distance, ending not far from lower tangent of median ocellus
2b) Flagellomeres	very short, shorter than their diameters	almost as long as their diameters
2c) Flagellomere II	little longer than first, but a little shorter than third	about twice the first, as long as third
3) No. hamuli	five	six
4) Comb and penicillus	weakly stiff	stiff
5) Body size	smaller	larger

Among these differences, items 2b and 5 are intimately correlated from each other (cf. Fig. 4 and Table 13). Fig. 4 gives similar correlations between body

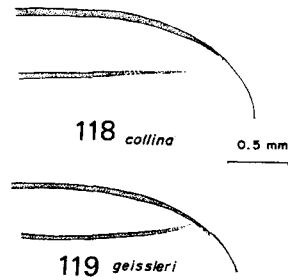
1) In the system by Wille and Michener (1973) the two subgenera can be called each *T. (Tetragona) iridipennis* and *T. (T.) atripes* group, and some species groups defined below are considered the sub-groups.

size and some other metric characters. Although less obviously, the head narrow relative to length (1a, 1c, cf. Table 8) and the shorter scape (2c, cf. Table 12) could be interpreted similarly. I assume that many if not all of the features by which *Tetragonula* is distinguished from *Tetragonilla* are allomorphic. Between two alternatives, whether smaller size is primitive or specialized, I adopt the latter. On the average stingless bees are much smaller than other apid bees (=sister groups) and anthophorid bees (=involving the groups related with the apid ancestor). Some stingless bees are virtually the smallest among bees. Possibly the ancestral stingless bees, or at least some lines of them, developed dwarfism in order to explore the unoccupied ecological niches, in particular, as to nutriment and nest sites. This dwarfism should have appeared from time to time in their descendants.¹⁾ However, *Tetragonilla* cannot be ancestral to the recent *Tetragonula* by the possession of a specialized feature, marginal cell rather broadly open at the apex, not almost closed as in *Tetragonula* (Figs. 118~119)²⁾. Therefore, two subgenera are considered monophyletic sister groups characterized each by a specialized feature:

	<i>Tetragonilla</i>	<i>Tetragonula</i>
Marginal cell	widely open (=specialized)	almost closed (=primitive)
Body size	relatively large (=primitive)	small (=specialized) with allomorphic changes, especially shortening of antennal segments

Shortening of antennal flagella linked with dwarfism is seen in some other groups consisting of small-sized species, e.g. *Trigonella* (Sakagami 1975) and some groups of *Hypotrigona* s. lat. (Moure 1961), suggesting a parallelism.

Trigona (*Hypotrigona*) *eocenica* described by Kelner-Pilault (1970, cf. also 1969) from the Eocene Baltic Amber resembles *Tetragonula* by some features, first of all, by emphatically projected mesoscutellum. By this peculiarity *T. eocenica* certainly does not belong to *Hypotrigona*, the structure of mesoscutellum-metanotum-propodeum of which is just opposite to that of *T. eocenica*. Moreover, *T. eocenica* is similar to *Tetragonula* by the posterior margin of pterostigma apically slightly concave and gradually tapering, not convex as in *Hypotrigona*. Size is comparable to *Hypotrigona* species, but also to *T.*



Figs. 118~119. Apex of marginal cell in *T. (Tetragonilla) collina* and *T. (Tetragonula) geissleri*.

1) Obviously this does not simply mean that recent groups involving small species are all specialized. *Plebeia* is regarded as a primitive group (Wille 1962, '63, '64), but the species are on the average smaller than those of many other groups. *Melipona* is highly specialized in many aspects, despite involving the largest stingless bees.

2) In two large workers of *T. fuscobalteata* from Taman Negara (cf. Fig. 110), marginal cell was completely closed, in one worker in the left wing, in another in both wings.

fuscobalteata. On the other hand, *T. eocenica* differs from *Tetragonula* by emphatically swollen hind basitarsus and, according to the author, by edentate mandible and metallic mesosomal coloration. Probably this fossil species represents an offshoot independent of both *Tetragonula* and *Hypotrigona*. The subgeneric name *Kelneriapis* nov. is proposed for its reception. Anyhow, this species indicates the appearance of a dwarfism combined with over-roofing mesoscutellum already in the Eocene.

Next, relations among the species of *Tetragonula* are analysed. First the specialized (apomorphic) and primitive (plesiomorphic) states of adopted characters were sought as far as possible and listed in Table 33. Some remarks concerning the table:

1) Assuming allomorphic changes along dwarfism, the trends given in Tabs. 4~15 and Fig. 4 could be used to infer the states of some metric characters. For instance, WL_2/HW , HTL/HW , LOD/MOD , GW/EW , SC/EL , FL/FW , ML/FW are generally regarded as primitive when large, and HTL/WL_2 , EL/MOD , IOD/OD

Table 33. Primitive and specialized alternatives of some diagnostic characters

Character	Primitive state (P)	Specialized state (S)
Worker characters (*=more or less common to males)		
1. General coloration	basically dark	partly or wholly pale
2. Color of antenna below	pale	dark
*3. Mesoscutal hairs	not well banded	well banded
*4. Frontal hairs	not or less plumose	plumose
*5. Body size	large	small
6. Gena	wide	very wide
7. Occiput	narrow	wide
*8. SC/EL	large	small
*9. FL/FW	large	small
Male characters		
10. Mandible	normal	receded
11. HTW/HTL	large	small
12. Pilosity of hind tibia	relatively long and partially sparse, with admixture of plumose hairs	homogeneously short and dense with no admixture of plumose hairs
13. Metasoma	as wide as or narrower than head	wider than head
14. T_7 dorsally	simple	Y-ridged
15. T_7 apically	rounded	pointed
16. Gonostylus arising from	lateral side of gonocoxite	dorsum of gonocoxite
17. Gonostylus	rod like, moderately wide	blade like (S_1) very slender (S_2)
18. Apex of gonocoxite	simple	clavate
19. Penis valve	horn like	blade like (S_1) very robust (S_2)

when small. But these are not included in the table, because a) correlations are only general, being inadequate to deal with particular species or species groups precisely, 2) changes along the trends are continuous, being inadequate to separate species groups. However, some species exhibit marked deviations from general trends, or, some metric characters change, particularly in males, discontinuously. These were cited in Table 33.

2) For characters given in Table 33 the primitive state was assumed by comparing the situations in other stingless bee groups and, if possible, in other bees. A state widespread in other groups or in other bees was considered primitive. For most male characters, comparison with other bees was impossible by high specialization of male characters. As males are not or only incompletely studied in many groups, statements given in Table 33 should be confirmed by further studies.

3) Character 6: According to allomorphic trends, a narrower gena is regarded as specialized, but an unusually wide gena, which is considered in bees and other Aculeata the specialized state, is also regarded here as specialized, i.e. as a specialized deviation from a "general specialization trend". Although not adopted here, unusually long malar space in some groups also could be a specialization, even though it deviates from an allomorphic trend.

4) Table 33 specifies the simpler type of male hind tibia as a specialization. This is supported by the fact that the alternative state, e.g. the type somewhat similar to female tibia is more widespread in stingless bees. But this is also explained by the following hypothesis: Genetic mechanism responsible for realization of corbiculae in female hind tibia, one of the most important diagnostic features of the Family Apidae, should affect also male tibia, inducing somewhat similar disposition. But this apparently useless condition would be eliminated later in some groups, resulting in the appearance of simple disposition. An alternative hypothesis, which considers the simpler type primitive, is possible but less likely, because a) queen hind tibia is also not corbiculated, b) structure of male hind tibia is so modified from that of anthophorid bees that the simple type cannot be an anthophorid reminiscence. The hypothesis might explain also the facultative occurrence of corbiculated male tibia in bumblebees, occasionally optional even within the same subgenus, though here the corbiculated type seems not so widespread than the simpler one. Franklin (1954) thought the corbiculated male tibia as functional and as a specialization under severe climate. But this assumption is not supported by biological evidence.

5) Some characters are not included in Table 33 as primitive and specialized states of which are difficult to determine. Among these S_5 and S_6 are most important and must be restudied in future. As stated in p. 190. S_5 (Figs. 70~73). of five small species is similar in disposition (=Type A in Table 34) whereas three large species possess each particular disposition (=Type B). It is possible to assume type A as primitive, from which other B types derived. The relatively long pregladular area in A, which can be considered primitive in bees, favors this interpretation. As seen in Table 34, however, this is not compatible with another interpreta-

tion supported by coincidence of more characters. Possibly type A is a convergence due to dwarfism. The fact which favors this assumption is the structure of S_6 . In small species, antecosta of S_6 is more or less distinctly curved and the apical process is short (Figs. 74~81). It is not unlikely that this tendency is associated with structure of S_5 , which covers S_6 in natural disposition.

Table 34. Distribution of character states in eight species known by both sexes.
P=primitive, S=specialized, p, sp, s=intermediate; L, S=large and small,
ls=intermediate; *=mainly in males; A, B, etc. cf. in text.

Species	Characters given in table 33															Characters not given in table 33			Descending body size by	
	3	4	8*	9*	10	11*	12	13	14	15	16	17	18	19	S_5	S_6	HTL*/HW	HTL*/WL ₂	HW	WL ₂
<i>iridipennis</i>	S	s	S	S	P	P	P	P	S	S	S	S ₁	P	S ₁	A	A	ls	L	7	7
<i>pagdeni</i>	S	S	S	S	P	P	P	P	S	S	S	S ₁	P	S ₁	A	A	ls	L	5	6
<i>fuscobalteata</i>	S	S	S	S	P	P	P	P	S	S	S	S ₁	P	S ₁	A	A	ls	L	8	8
<i>geissleri</i>	P	P	S	P	P	sp	P	S	P	S	P	S ₂	P	S ₂	B ₁	B	L	L	2	1
<i>laevipes</i>	P	P	s	sp	P	S	S	P	P	P	P	P	P	P	A	A	S	S	3	3
<i>hirashimai</i>	S	s	S	sp	P	S	S	P	P	P	P	P	P	P	B ₂	B	S	S	1	2
<i>pagdeniformis</i>	S	s	s	sp	P	S	S	P	P	P	P	P	P	P	A	A	S	S	6	5
<i>gressitti</i>	P	S	P	sp	S	S	S	P	P	P	P	P	S	P	B ³	B	L	L	4	4

Table 34 presents distribution of character states in eight species known by both sexes, accompanied with conditions of some other characters for which primitive and specialized stages were not determined. From the table, the following species groups are recognized:¹⁾

I. *iridipennis* group: Characterized by state S in characters 3, 4, 8, 9, 14, 15, 16 17 (S_1), 19 (S_1) and P in 10, 11, 12, 13, 18, where 9, 14, 16, 17 are autapomorphic and 11 is primitive only in this group. States of no adopted characters vary within the group. Besides, S_5 and S_6 are type A, HTL/WL₂ is relatively large and HTL/HW intermediate only in this group. Included species; *T. iridipennis*, *T. pagdeni*, *T. fuscobalteata*.

II. *geissleri* group: Characterized by state S in characters 8, 13, 15, 17 (S_2), 19(S_2), sp in 11 and P in 3, 4, 9, 10, 12, 14, 16, 18, where 13, 17, 19 are autapomorphic. Besides, S_5 is type B₁, S_6 =B. HTL/HW and HTL/WL₂ large. Included species: *T. geissleri*.

III. *laevipes* group: Characterized by state S in characters 8, 11, 12, sp in 9 and P in 10, 13~19. No characters are strictly autapomorphic but 8 can be regarded as such, assuming its apomorphic state in other groups as parallelism. S_5 and S_6 variable. HTL/HW and HTL/WL₂ small only in this group. Included species: *T. laevipes*, *T. pagdeniformis*, *T. hirashimai*.

1) Citation of primitive state might not be allowed by the strict Hennigian procedure. But in practice it facilitates distinction of the groups.

IV. *gressitti* group: Characterized by state S in characters 4, 10, 11, 12, 18, sp in 9 and P in 3, 8, 13~17, 19, where 10 and 18 are autapomorphic. No characters are P only in this group. Besides, $S_5=B_3$, $S_6=B$ and HTL/HW and HTL/WL₂ relatively large. Included specie: *T. gressitti*.

Concerning phyletic relations among these groups, *T. gressitti* certainly close to *T. laeviceps* group. Or, the latter might be defined better, including *T. gressitti*, by autapomorphic state of character 12. A monospecific group was erected by extreme specializations in character 10 and 18 in spite of relatively long scape. Relations among other groups are not clear. Excluding the characters represented by autapomorphic states in some groups, table 34 is condensed:

Species groups	Characters				
	8	9	11	12	15
I. <i>iridipennis</i>	S	S	P	P	S
II. <i>geissleri</i>	S	P	sp	P	S
III. <i>laeviceps</i>	S	sp	S	S	P
IV. <i>gressitti</i>	P	sp	S	S	P

Assuming the minimum number of parallelisms three cases in Fig. 113 are equally likely, which postulate parallel evolution in some of characters 8, 9, 11 and 12. But the number of adopted characters is only five and the minimum number of parallelisms is three. Unless the number of reliable characters is higher, the difference between the minimum (3) and maximum (5) is too small to make a persuasive interpretation. Moreover, most characters are metric, and states S and P can be determined only arbitrarily. The presented cladograms should be regarded as touchstones to be confirmed or rejected by further studies.

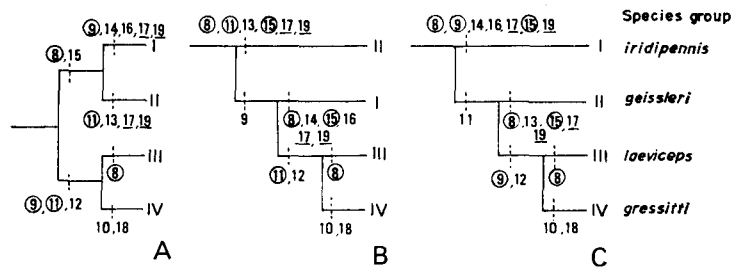


Fig. 120. Three possible cladograms showing relation of four species group. Annexed numerals on stem=specialized stage of characters numbered in Tabs. 33 and 34. Circled=parallel evolution. Underlined=divergence.

Anyhow, the figures suggest the appearance of advanced dwarfism at least twice independently, in *iridipennis* and *laeviceps* groups. The different behavior of these two groups in allomorphic series (Fig. 4), especially in WL₂/HW, HTL/HW and ML/FW, favors this assumption. Fig. 114 visualizes the relations among HW, WL₂

and HTL given in Figs. 1~3 by triangular diagram. Assuming the position of *T. (Tetragonilla) collina* as the starting point of dwarfism, *T. geissleri* and *T. gressitti* workers are characterized each by relative increase and decrease of HTL, whereas *laeviceps* group by decrease of WL_2 compensated by increase of HW. This tendency is more conspicuous in *iridipennis* group. By this difference, two groups are located as separate clusters. The discussion given above suggests this tendency as a parallelism, not a monophyletic trend (cf. Fig. 4, WL_2/HW)¹⁾. In males, too, *iridipennis* group is shorter-winged than *laeviceps* group, but here compensated by increase of HTL, not of HW, despite male HTL is proportionally shorter than in conspecific worker in all species except *T. gressitti* (cf. Fig. 5).

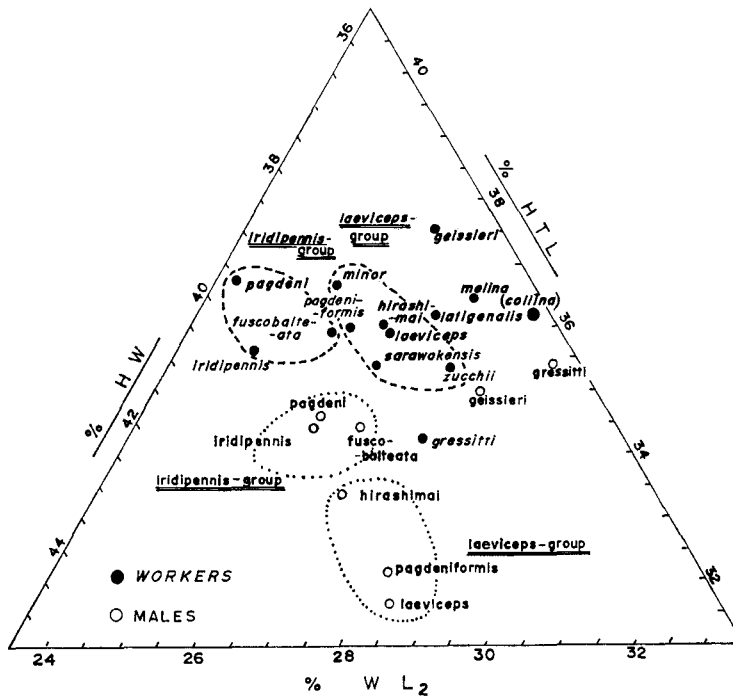


Fig. 121. Triangle diagram showing relation HW, WL_2 and HTL in various *Tetragonula* species and worker of *T. (Tetragonilla) collina*.

Within *iridipennis* group *T. pagdeni* and *fuscobalteata* are certainly closer for each other. From this couple, *T. iridipennis* is more distant and more specialized by wider gonostylus and penis valve. Within *laeviceps* group, *T. hirashimai* and *pagdeniformis* are more specialized by formation of mesoscutal bands, and possibly

1) Advanced brachypterism does not necessarily relate with dwarfism. *Melipona*, including the largest stingless bees, is conspicuously short-winged.

by subapical dilation of gonostylus, but their interrelation is uncertain. Concerning the species known by worker alone, *T. zucchini*, *sarawakensis* and *minor* may belong to *laeviceps* group by their general similarities in worker characters. *T. melina*, specialized in body coloration, might belong to *geissleri* group, especially by its long hind tibia. *T. latigenalis* may represent its own group by advanced macrocephaly. Its gena is even wider than in *T. (Tetragonilla) collina* (Fig. 4, Table 10).

Geographic distribution

Table 35 presents the geographic distribution of each species in terms of the number of records (cf. Appendix). The figures at the top shows the relative intensity of collecting in various areas, being most intensive in Malaya, followed by N. Thailand, Sri Lanka, S. Thailand, India and Viet Nam. The materials are insuffic-

Table 35. Geographic distribution of various species shown by the number of collecting records in each area. "+" cited from Schwarz (1939).
HW=the descending order of mean HW (cf. Table 1)

Areas	Singapore	Malaya	Pen. Thailand	S. Thailand	Cambodia	E. Thailand	Viet Nam	Laos	N. Thailand	Tenasserim	India	Andaman Is.	Sri Lanka	Total No. records	HW
Total No. records	5	54	18	29	2	5	25	7	37	1	28	1	29	241	
<i>zucchini</i>		8												8	5
<i>sarawakensis</i>	1	2	+											3	6
<i>minor</i>		1												1	12
<i>pagdeniformis</i>		12	2											14	10
<i>latigenalis</i>		5	1											6	1
<i>melina</i>		1	1											2	4
<i>geissleri</i>	1	5		1										7	3
<i>fuscobalteata</i>		9	2	3		+			2					16	13
<i>laeviceps</i>	3	39	8	6	+	2	23	3	16					100	7
<i>pagdeni</i>			8	24	2	3	1	1	17	1				57	9
<i>gressitti</i>							4							4	8
<i>hirashimai</i>									13					13	2
<i>iridipennis</i>											28		29	57	11
forma UB						1		1						2	
TK						1		1						2	
BG											1			1	
BGA												1			
No. species	3	9	7	4	2	2	4	2	4	1	1	0	1	13	
						+		+			+	+		+	
						2		2			1	1		4	

ient in other areas, in particular, Cambodia and Tenasserim. The areas virtually unexplored are Burma and the northern half of Viet Nam, by which we do not know the northern limit of *Tetragonula* in the coastal area of the Continent, and the boundary between two closely similar allopatric species, *T. iridipennis* and *pagdeni*. The number of species is richest in Malaya, followed by Peninsular Thailand and gradually scarcer northward. The righthand column shows that Malaya and P. Thailand have the species variable in body size, i.e. those probably occupying different niches, which indicates a higher diversity in biofaunistic makeup. The most widespread and probably commonest species is *T. laeviceps*, followed by *T. pagdeni* and *fuscobalteata*. *T. iridipennis* is geographically isolated from other species, virtually monopolizing the Indian subcontinent.

Miscellaneous notes

1. **Variation of the number of hamuli:** Moure (1961) considered the number of hamuli per wing a group character (cf. p. 230). Schwarz (1948) made variation analysis of the number of hamuli per wing in many social bees, including some *Tetragonula* species. Variation of the number of hamuli per left wing was examined in various species (Table 36). The percentage anomaly varies from species to species; 0.0% in some species while attaining 30% in workers of *T. gressitti* and *hirashimai*. In *T. melina* all three workers had incidentally six hamuli.

Table 36. Variation in the number of hamuli per left wing. The species are arranged in the descending order of mean WL_2 in workers

Species	Workers No. hamuli ¹⁾						Males No. hamuli ¹⁾					
	N	4	5	6	7	$\frac{0}{0}^{(2)}$ anomalies	N	4	5	6	$\frac{0}{0}^{(2)}$ anomalies	
<i>latigenalis</i>	18		18			—						
<i>melina</i>	3			3		100.0						
<i>geissleri</i>	71		71			—	19		19		—	
<i>zucchii</i>	24		20	0/6		0/25.0						
<i>hirashimai</i>	27		19	4/4		0/29.5	61	1/1	54	3/2	3.3/8.0	
<i>sarawakensis</i>	10		10			—						
<i>laeviceps</i>	563	8/1	499	23/31	1/0	1.6/8.9	18	0/1	17		5.5/0	
<i>gressitti</i>	20		14	5/0	0/1	0/30.0	2		2		—	
<i>pagdeniformis</i>	27	2/1	24			1.1/0	117	1/0	111	2/3	0.8/4.3	
<i>pagdeni</i>	249	5/1	234	5/4		2.4/3.6	75	2/0	72	1/0	2.7/1.3	
<i>minor</i>	32		32			—						
<i>iridipennis</i>	153		135	15/3		0/11.8	109	1/0	96	6/6	0.9/11.0	
<i>fuscobalteata</i>	134		134			—	62	1/0	61		1.6/0	

1) In anomalous cases ($n \neq 5$), the frequencies are separately given as (A/B) for the wings shorter than, or longer than mean WL_2 .

2) % ratios of $n < 5$ and $n > 5$ are separately given by A'/B'.

Percentage anomaly for all examined specimens is 8.87% ($4=0.98$, $6\sim7=7.89$) in workers and 6.70% ($4=1.73$, $6=4.97$) in males. No significant difference was observed between anomaly and mean WL_2 in all species. In both sexes supernumerary cases (6, 7) were more frequent. In social bees the number of hamuli roughly correlates with wing length. If my interpretation, dwarfism as a general trend in *Tetragonula* (p. 231) is valid, frequent supernumerary could be a primitive condition. Interestingly, *T. (Trigonella) moorei* Schwarz, a species about as large as *T. laeviceps*, retains the number of hamuli on the average as high as *T. collina*, i.e. among 52 workers, $5=1$, $6=31$ and $7=20$, against $6=33$, $7=16$, $8=1$ in 50 examined workers in the latter.

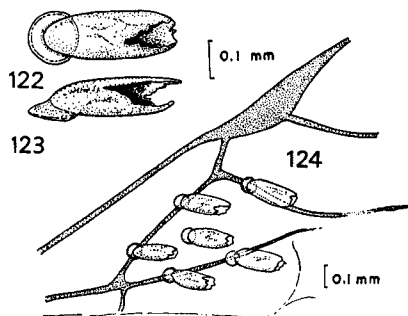
2. Geographic size gradient: Some widespread species exhibit a size gradient, being larger in northern areas. This was observed in *T. laeviceps*, *pagdeni*, *iridipennis* but not in *T. fuscobalteata*. In a previous paper the northward increase of body size was detected in *T. (Tetragonilla) collina* Smith (closer analysis not published), *T. (Tetrigona) apicalis* Smith, *T. (Lepidotrigona) ventralis* Smith, but not in *T. (L.) terminata* Smith. Although the number of specimens was scarce, an opposite tendency was suggested in *T. (Lophotrigona) canifrons* Smith. Further studies are necessary, but many if not all species seem to increase their size in northern areas. The similar trend is known in the European honeybee (Alpatov 1929). In the Asiatic honeybee, too, *A. cerana cerana* Fabricius in Japan and China is distinctly larger than *A. c. javana* Enderlein (S.E. Asia) and *A. c. indica* Fabricius (India). It is interesting that these highly eusocial bees, being homoiothermal as the colony, behave as if following Bergman's rule.

3. Notes on males: Systematic studies of stingless bees have been obstructed by the scarcity of male specimens. Certainly total number produced of males per colony per period may be lower than that of workers, but the males should not be so rare as represented in museum collections. As in some blood sucking dipterans, the scarcity of males must depend on their peculiar habits. In many Neotropical species observed by Dr. R. Zucchi and by myself, callow males stay a considerable time in nests. Once having left nests, their subsequent behavior seems variable according to species or supraspecific groups (cf. Kerr et al. 1962). Closer comparison and classification of habit types are required, but in many species males seem to form an aggregation, and to practice mass flight near the nests. Pagden (1957) observed such in *T. fuscobalteata*, *iridipennis* ($=T. laeviceps$ in the present paper), *T. atripes collina* ($=T. collina$ in the present paper) and *T. apicalis* in Malaya, occasionally forming a swarm of several thousands. He recommended to catch these males together with workers from the same nest to associate both sexes. Obviously it is ideal to collect both from the inside of the same nest. In this case, however, males are often young and their coloration is not yet fully pigmented. In the materials used for the present study, too, males were represented in most species only by one lot or two, but each lot often by many specimens: *T. geissleri* (22 ♂ from one nest), *T. hirashimai* (62 ♂ in a single lot), *T. laeviceps* (9, 1, 2, 4 ♂ in four lots), *T. gressitti* (1 and 1 ♂ in two lots), *T. iridipennis* (113 ♂ in

a single lot), *T. pagdeniformis* (124 ♂ in a single lot), *T. pagdeni* (53 and 39 ♂ in two lots), *T. fuscobalteata* (56 and 5 ♂ in two lots).¹⁾

Dr. Y. Miyatake, who collected males of *T. hirashimai*, *T. pagdeniformis* and *T. pagdeni* (Kor Hong) wrote me the following observations: "These swarms were collected at the clearings of secondary forests, the nearby presence of nests was not noticed. Interestingly the swarms involved some bugs and syrphids which were closely similar to the bees". The occurrence of insects mimic to stingless bees is known also in South America (Schwarz 1948, Kerr et al. 1967). In these cases, however, mimicry should be somewhat different from that between other bees and wasps bearing functional stings and their mimics. Some stingless bees, particularly of the Neotropical Region, are very aggressive but only at defense of nests. Foragers on flowers are inoffensive. Mimicry may be effective only when the mimics live near the nests.

Sixteen out of 53 males of *T. pagdeni* from Kor Hong bore empty cocoons of some parasite on the underside of fore wings. Cocoons (Figs. 122~124) were semitransparent, about 0.35 mm long and 0.15 mm wide, attaching by means of an expanded skirt of the rear end to the veins or membrane of the middle part of the fore wing, more than half to vein *M*. The distal end bore an irregular emergence hole. The number of cocoons per bee was distributed (R, L=right and left wings): 1 (4 cases: 1/R=1, 1/L=3), 2(5: 2/R=2, 1/R+1/L=3), 4(3: 2/R+2/L=3), 5 (1: 2/R+3/L), 6 (1: 2/R+4/L), 7 (1: 1/R+6/L), 9 (1: 3/R+6/L, Fig. 117).



Figs. 122-124. Cocoons found on wings of some males of *T. pagdeni*. 122 and 123. dorsal and profile view. 124. Attachment of cocoons to fore wing.

Summary

The stingless bees belonging to the subgenus *Tetragonula* Moure (= *Trigona iridipennis* group) of the Continental Asia and Sri Lanka are revised. Thirteen species including six new species are recognized. The species known by both sexes are classified in four species groups. *T. iridipennis* Smith, the type species, previously known as widespread from Sri Lanka, India to Solomon Islands, is redefined as confined to India and Sri Lanka, which belongs to the species group being different from that to which *T. laeviceps* Smith (= *T. iridipennis* in S.E. Asia in previous usage) is involved.

1) By this fact the variation ranges in males would have been underestimated than in workers.

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- Zeuner, F. E. and F. J. Manning 1976. A monograph on fossil bees (Hymenoptera: Apoidea). *Bull. Brit. Mus. (Nat. Hist.) Geol.* **27**: 155-268, 4 pls.

Appendix: Sources of the specimens examined

- AMNH=American Museum of Natural History, New York.
 BMNH=British Museum (Natural History), London.
 BPBM=Bernice P. Bishop Museum, Honolulu.
 NMSI=National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 EKOU=Entomological Laboratory, Kobe University, Kobe.
 EKYU=Entomological Laboratory, Kyushu University, Fukuoka.
 EZAB=Division of Entomology and Zoology, Department of Agriculture, Bangkok.
- The locality names given in the annexed labels are cited without modifications.

SINGAPORE

Singapore -1. Nee Sung Forest Reserve, xii 7 1958, T.C. Maa (BPBM); -2. Bukit Timah, xii 12 1974, T. Kawamichi (Nest C in post of an office); -3. University of Singapore, iii 29 1975, T. Kawamichi (two nests, A,B, 50 cm distant for each other in window frames); -4. Singapore, H.N. Kidley 97-203 (BMNH); -5. Singapore, ix 22 1932, S. Matsumura (Entomological Institute, Hokkaido University).

MALAYA

Pasoh (Pasoh IBP Station, Negri Sembilan). viii 1974, T. Kawamichi (visiting fruit juice).

Kanching (115 miles N Kanching, Selangor). i 14~15 1930, H.M. Pendulbury, 1955-354 (BMNH).

Subang (Subang Forest Reserve, Selangor). 900~120 m, iii 12~14 1958, T.C. Maa (BPBM).

Kepong (Kepong Forest Reserve, Selangor). 90~180 m, iii 12 1958, T.C. Maa (BPBM).

Ulu Langat (Selangor), vi 13~14 1958, T.C. Maa (BPBM).

Kuala Lumpur -1. 40 km N of Kuala Lumpur, 350~400 m, 16 ix 1961, J.L. Gressitt (BPBM); -2. Ampang Reservoir, ix 23 1966, Sh. F. Sakagami, K. Yoshikawa and R. Ohgushi; -3a. ii 24 1928, swarming, H.T. Pagden (AMNH); -3b. vii 22 1922, H. T. Pagden, Acc. 36603 (AMNH); -3c. iv 11 1936, Acc. 36603 (AMNH); -3d. Univ. Malaya Campus, viii 30 1968, R. Jander; -3e. ix 14 1964, Y. Hirashima (EKYU); -3f. viii 11~15 1926, at light, H.M. Pendulbury (BMNH); -3g. vii 22 1922, H.M. Pendulbury, 1955-354 (BMNH); -3h. iv 11 1936, Acc. 36603 (AMNH).

Gombak (=University of Malaya Gombak Reserve near Kuala Lumpur)-a. ix 1 1968 lot S-6; -b. ix 20 1968 lot S-12; -c. vii 21 1970, lot 4; -d. vii 31 1970, lot 6, all R. Jander; -e. xi 8 1963, Y. Hirashima (EKYU).

Templer Park (Selangor). -a. ix 20 1966, Sh. F. Sakagami, K. Yoshikawa and R. Ohgushi; -b. ditto, from nest; -c. xi 14 1964, Y. Hirashima (EKYU).

Fraser's Hill (Fraser's Hill Gap, Pahang-Selangor) -a. ix 15~16 1966, Sh. F. Sakagami; -b. ix 12~16 1968, lot S-8; -c. viii 16 1970, lot 8, both R. Jander.

Fentung Sempak -a. vii 12 1970, lots 1 and 2; -b. vii 21 lot 4, 1970, all R. Jander.

Taman Negara. viii 24, 1970 lot 9, R. Jander.

Kuala Tahan -a. Kuala Tahan, King George V National Park, xii 12~17 1958, T.C. Maa (BPBM); -b. ix 24~29 1968; -c. viii 31 1970, lot 12, both R. Jander.

Gua Che Yatim (King George V National Park, Pahang). xii 1958, J.L. Gressitt (BPBM).

Kuala Tranggan (King George V National Park). 200 m, xii 15~17 1958, T.C. Maa (BPBM).

Bagan Tiang -a. Bagan Tiang, Krian, iii 27 1931, at male flowers of *Typha*, H.T. Pagden (BMNH); -b. Perak, MFS. Krian, Sureo Lee Estate, on flower of "*Thypha angustifolia*", iii 18 1931, H.T. Pagden (BMNH); -c. Swe Lee Estate, xi 18 1931, ♂ *Thypha angustifolia*, H.T. Pagden (BMNH).

Tahan River (lef bank 300'). xi 29 1929 (AMNH).

Pulan Jarak (W. Coast) -a. iv 12 1932, Acc. 36603 (AMNH); -b. iv 12~15 1932 (BMNH), both E. Seimund.

Tapah. ix 26 1966, Sh. F. Sakagami, K. Yoshikawa and R. Ohgushi (nests).

Cameron Highland (Pahan State) -a. Mt. Brinchang, 2030 m, i 1~9 1959, L.W. Quate (BPBM); -b. ix 28 1966, K. Yoshikawa, R. Ohgushi and Sh. F. Sakagami.

Bukit Mertajam. x 3 1966, Sh. F. Sakagami.

Penang -1. Sungei Pinang, nest in *Spondias erythrea*, -1a. vi 9 1957; -1b. ix 11 1956, resting mass, nest entrance; -1c. Sungei Pinang Hills, iii 11 1954, ex nest in *Spondias erythrea*; -1d. viii 11 1958, Sungei, nest in Rambutan; -1e. ix 21 1956, collecting batumen, all H.T. Pagden (BMNH); -2. Batu Feringgi, x 25 1956, H.T. Pagden (BMNH); -3. Mr. Eokine Road, vii 12 1955, at *Memecylon umbellatum*, H.T. Pagden (BMNH); -4. Penang Hill, 2000 ft, iii 9 1947, *Ageratum*, R.A. Lever (BMNH); -5. Botanical Garden, Georgetown -5a. x 3 1966, Sh. Sakagami, K. Yoshikawa and R. Ohgushi; -5b. x 3-4 1968 R. Jander.

PENINSULAR THAILAND

Yala. vii 8 1961, lot Th-192, Kamol (EKOU).

Satun (Satun Road, Satun Prov., E. Boundary). i 1964, G.A. Samuelson (BPBM).

Nakorn Sritamaraj. -a. vii 13 1961, visiting gum tree, K. Iwata (EKOU); -b. (Nakon Sri Tanarat), v 7 1928 (AMNH).

Ban Prakamp (Songkhla Prov.). vii 18 1928, J.L. Gressitt.

Songkhla-a. (Singora), vi 29, H. Smith (AMNH); b. Songkhla, xi 1 1939, lot 621, A. Susaorus (EZAB); -c. i 29~30 1962, A. Nagatomi and S. Nakao (EKOU); -d. vi 26 1965, Y. Miyatake (EKYU).

Kor Hong. vi 23 1965, Y. Miyatake.

Patalung (Rice Exp. Sta.). vii 11 1961, K. Iwata.

Trana. Lot 2729, iv 7 1960 (EZAB).

Khao Chong -1. Khao Chong Park, iii 1 1965, K. Yasumatsu (EKYU); -2. Khao Chong nr. Trung, iv 26 1965, Y. Miyatake (EKYU).

Khaophappa-Khao Chong (200-400 m, Trang Prov.). xii 16 1963~i 11 1964, G. A. Samuelson.

Banna (Banna-Nakhorn, 108 m). v 5~10 1958, T.C. Maa (BPBM).

Naborn. -1. vii 16 1961, lot Th 190, K. Iwata (EKOU); -2. Chwang nr. Nabon, 70 m, ix 5 1958, T.C. Maa (BPBM).

SOUTHERN THAILAND

Chantaburi-Prew a. v 5 1938, lot 561; -b. ix 4 1963, lot 2908; -c. Ban Ang, xii 6~17 1955, lot 1965, all P. Pholboon (EZAB); -d. iv 24~v 1 1958, T.C. Maa (BPBM); -e. iv 20 1961, from nest entrance, lot Th 205, K. Iwata (EKOU); -f. iv 20 1961, on male palm flowers, lot Th 214, K. Iwata (EKOU); -g. Prew Exp. Sta., i 18 1963, S. Nakao (EKOU); -h. i 22 1963, A. Nagatomi (EKOU); -i. Prew Exp. Sta., x 12 1966, from nest, Sh. F. Sakagami and K. Yoshikawa; -j. xi 29~30 1973, Y. Hirashima (EKYU).

Hua Hin (Prachuab Prov.). xii 9 1937, lot 501 (EZAB).

Kanchanaburi. xii 10 1935, lot 258, C. Tongyai (EZAB).

Skiracha. xi 15 1961, A. Nagatomi (EKOU).

Cholburi (Song Phra, Cholburi). ix 2 1936, lot 335, C. Tongyai (EZAB).

Bangkok -a. xii 2 1936, lot 356, Pae (EZAB); -b. iii 16 1937, lot 407, S. Cooptawathin (EZAB); -c. xii 23 1959, lot 629, P. Pholboon (EZAB); -d. iii 5 1961, lot Th 342, nesting in house wall, K. Iwata (EKOU); -e. iii 5 1961, visiting *Crescentia cujeta*, lot Th 344, K. Iwata (EKOU); -f. iv 4 1961, lot Th 209, Hidaka (EKOU); -g. iv 6 1961, visiting Euphorbiaceae, K. Iwata (EKOU); -h. xi 9 1962, A. Nagatomi (EKOU); -i. xii 7 1964, R. Ohgushi (EKOU); -j. vii 28 1971, T. Tano; -k. x 26 1966, nesting in rest house posts, Sh. F. Sakagami and K. Yoshikawa; -l. i 13 1937, lot 387, P. Pholboon (EZAB).

Saraburi. v 26 1938, lot 548, Ekasak (EZAB).

Kamphangpet. xii 26 1957, T. Umehao, K. Yoshikawa and K. Yada.

Korat. iii 20 1958, K. Yoshikawa.

EASTERN THAILAND

Ubol. xii 20 1962, S. Nakao (EKOU).

Kamcha (Kamcha Eé). xii 21 1962, A. Nagatomi (EKOU).

Mukadaharn. xii 22 1962, nesting in telegraph pole, S. Nakao (EKOU).

Nakom Phanom (Pupan National Park). ii 26 1965, K. Yasumatsu (EKYU).

NORTHERN THAILAND

Uthaithani. iv 13 1963, lot 2884 (EZAB).

Sam Ngow Tak. v 27 1959, lot 2522, W.S. Pansna (EZAB).

Lamphun. iv 1~2 1955, lot 1849, P. Pholboon (EZAB).

Chieng Mai -1. -1a. Chieng Mai Arboretum, 300 m, vi 12 1965, P.D. Ashlock (BPBM); -1b. xi 18 1963, lot 2880, P. Maceoti (EZAB); -1c. iii 11-12 1961, lot Th 336, K. Iwata (EKOU); -1d. Mae Nam River, lots Th 178, 212, 339, v 1 1961, K. Iwata (EKOU); -1e. v 11 1961, lot Th 151, K. Yoshikawa (EKOU); -1f. Mae Nam, v 5 1961, lot Th 201, K. Yoshikawa (EKOU); -1g. v 13 1961, lot Th 208, from nest in a post, K. Iwata (EKOU); -1h. iii 12 1961, K. Iwata (EKOU); -2. Ban Tub Dou nr Chieng Mai, x 19 1973, Y. Hirashima (EKYU).

Doi Suthep -1. -1a. 1278 m, iii 28~v 4 1958, T.C. Maa (BPBM); -1b. xi 18 1962, A. Nagatomi (EKOU); -1c. 1000 m, vi 12 1965, K. Morimoto (EKYU); -1d. xi 30 1963, K. Yasumatsu (EKYU); -1e. iii 12 1961, collecting gummi from leguminosae, K. Iwata (EKOU); -2. Tan Keo, 800 m, vi 10 1965, Y. Miyatake (EKYU).

Doi Dao. i 19 1958, T. Umesao.

Mae Klang -1. 340 m, v 11 1965, P.D. Ashlock (BPBM); -2. Mae Klang Water Fall nr Chom Thong, vi 11 1965, K. Morimoto (EKYU).

Mae Sa (Mae Sa Water Fall, Chieng Mai Prov.). vi 16 1965, Y. Miyatake (EKYU).

Mae Fak -1. Mae Fak, v 18 1958, Ikoma; -2. Mae Fak Dam, xii 12 1962, S. Nakao (EKOU).

Muang Fang-a. iii 15~v 15 1961, lots Th 204, 330, 331, 340, K. Iwata (EKOU); -b. iii 16 1961, lot Th 327, on Kaeslong flowers, K. Iwata (EKOU); -c. iii 16 1961, lot Th 203, on nest entrance, K. Iwata (EKOU).

Chieng Dao (Chieng Mai Prov.). -a. iii 29~v 4 1958; -b. 450 m, iv 5~11 1958; -c. vi 15 1958, all T.C. Maa (BPBM); -d. Chengdow, iii 14 1961, lots Th 334, 345, K. Iwata (EKOU); -e. iii 17 1961, lot Th 335, K. Iwata (EKOU).

Fang -1. -1a. 500 m, iv 12~19 1958, T.C. Maa (BPBM); -1b. xi 23~xii 2 1962, S. Nakao (EKOU); -1c. vi 14 1964, Y. Miyatake (EKYU); -2. Agricultural Exp. Sta., Fang, 600 m, -2a. vi 14 1965, P.D. Ashlock (BPBM); -2b. xi 23 1973, on *Helianthus*, Y. Hirashima (EKYU); -3. Montaneous environment, 1000~1200 m, xi 24 1973, Y. Hirashima (EKYU).

CAMBODIA

Oudong. ii 28 1958, K. Yoshikawa.

Kom Pom Cham. ii 20 1958, K. Yoshikawa.

VIET NAM (all BPBM)

Karyu Danar. 200 m, ii 13~28 1961, C.M. Yoshimoto.

Phan Thiet. xi 4~7 1960, C.M. Yoshimoto.

Blao (Balao) -1a. 500 m, x 14~21 1960; -1b. 600 m, x 14~21 1960; 2. 60 km SW Blao, 500 m, iv 22 1960, all C.M. Yoshimoto.

Phang Rang. (NW Phan Rang.) x 8~16 1960, C.M. Yoshimoto

Di Linh (Djiring) -1a. 1200 m, iv 22~23 1961; 1b. 900 m, ix 27~x 14 1960; -2. 9 km S Di Linh, iv 24 1960, all C.M. Yoshimoto.

Fyan- a. 900~1000 m, vii 11~viii 9 1961; -b. 1200 m, vii 11~viii 9 1961, both N.R. Spencer.

Dalat -1. 1500 m, 1a. iv 29~v 4 1960; -1b. ix 26~27 1960; -2. 6 km S Dalat, 1400~1500 m, vi 9~vii 7 1961; -3. 10 km S Dalat, 1300 m, ix 12 1960; -4. 20 km S Dalat, 1300 m, ix 12 1960, all J.L. Gressitt.

Ban Me Thout -1. 500 m, -1a. v 16~18 1960; 1b. xii 21~24 1960; -2. M'Drak E of Ban Me Thout 400~600 m, xii 8~19 1960, all C.M. Yoshimoto.

- Dak Song (76 km SW Ban Me Thout). 870 m, v 19-21 1960, C.M. Yoshimoto.
 Pleiku -1. 30 km NW Pleiku, 300 m, v 10 1960; -2. 20 km N Pleiku, 650 m, v 9 1960; -3. 700 m, v 8~14 1960; -4. 50 km SW Pleiku, 250 m, v 14 1960, all L.W. Quate.
 Kontum (N Pleiku). 550 m, v 13 1960, L.W. Quate.
 Dai Lanh (N Nha Trang). xi 30~xii 5 1960, C.M. Yoshimoto.

LAOS

- Pakse (Sedone Prov.). v 23 1965, P.D. Ashlock (BPBM).
 Thakhek -a. iii 9 1958, K. Yoshikawa; -b. iii 22 1958, K. Yoshikawa.
 Paksane (Borikane Prov.) -a. xi 19 1965; -b. xi 29 1965, both native collector (BPBM).
 Luang Prabang. 300 m, vi 11-12 1960, S. Quate (BPBM).
 Muong Sing (NW Luang Prabang). 650 m, vi 6~10 1960, S. Quate (BPBM).

TENASSERIM

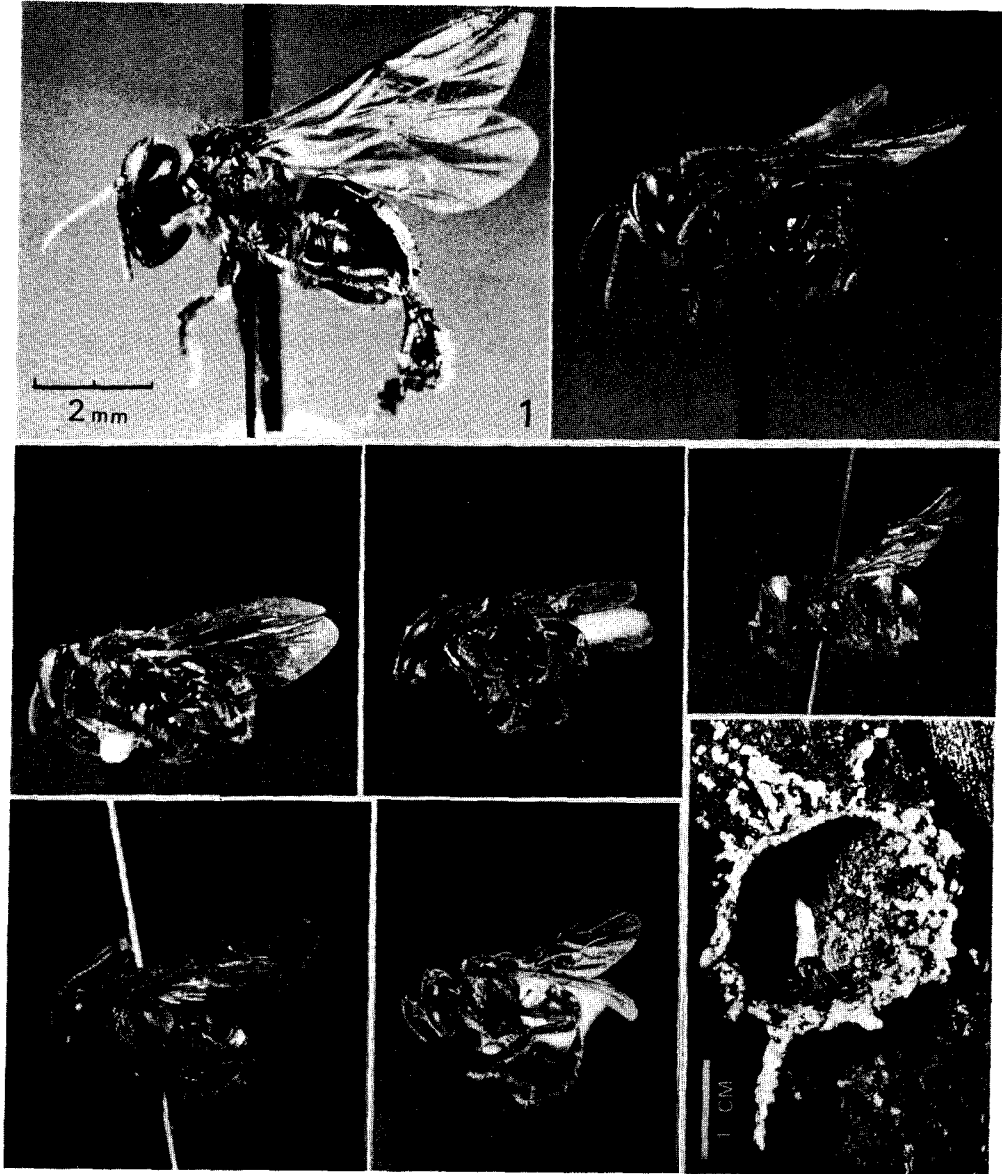
- Maul Maia, Tenasserim 2-94, Bingham coll., col. C.T. Bingham 96-30 (BMNH).

INDIA

- Dehra Dun (U.P.). vi 1974, from *Tecoma zephyranthes* and from a nest, P. Singh.
 Calcutta. Botanical Garden, Howrah, i 7 1974, R. Kudo.
 Bombay -a. xii 1904, Acc. 22954 (AMNH); -b. 1904, Cameron collection, 1914-10 (BMNH); -c. Marzazan, vii 21 1963, F.L. Wain.
 Poona (500 m) -a. x 29 1966; -b. viii 8 1966; -c. iv 1-4 1967; -d. i 14 1970; -e. i 24 1970; -f. ix 23 1971; -g. ix 27 1971; -h. x 12 1971; -i. xi 5 1971, all F.L. Wain.
 Lonavla (W. Ghats). i 13 1970, F.L. Wain.
 Nagpur. On *Cleome chelidionii*, 1956 (BMNH).
 Bangalore. xii 29 1973, R. Kudo.
 Madras -1. Adyar, vii 27-29 1963; -2. Loyola University Campus, -2a. viii 10 1973; -2b. xi 26 1973; -2c. xii 4 1973; -3. City Park, vii 9 1973, all R. Kudo.
 Kodaikanal (nr. Madras). viii 13 1973, R. Kudo.
 Krum Bagaram -a. Krum Bagaram, Karikal, P.S. Nathan, pres. by W.S. Bronley, 1949-193 (BMNH); -b. Kurum Bagaram, Karikal, S. India, P.S. Nathan (AMNH).
 Pathanapuram (Kerala). iii 21 1970, F.L. Wain.
 Alwaye Khiaskam (Balar, Kerala). xi 39 1971, F.L. Wain.
 Andaman Islands. G. Rogers 1906-204 (BMNH).

SRI LANKA (all NMSI except Colombo-b, Hambantota and Thwaites)

- Colombo (Col. Dist.) -a. x 29~30 1969, P.B. Karunaratne; -b. viii 12 1961, F.L. Wain;
 -c. Museum Garden, v 28~31 1975, K.V. Krombein, P.B. Karunaratne and P. Fernando.
 Labugama (Col. Dist.). Labugama Reservoir Jungle, x 13~14 1973, K.V. Krombein, P.B. Karunaratne, P. Fernando and J. Ferdinando.
 Elephant Pass (Jef. Dist.). x 23 1969, K.V. Krombein and P.B. Karunaratne.
 Enselwatte (Mat. Dist.). v 25 1975, S.L. Wood and J.L. Petty.
 Nalando (Mat. Dist.) iii 4 1972, K.V. Krombein and P.B. Karunaratne.
 Sigiriya (Mat. Dist.). 800 ft, ii 25 1970, Davis and Rowe.
 Trincomalee (Tri. Dist.) China Bay, Bungalow, 0~100', v 12~15 1976, K.V. Krombein, P.B. Karunaratne, D.W. Balassoriya (Malaise trap).
 Hambantota. S.P. ii '08, Coll. T. BF. AAFK, T.B. Fletcher (BMNH).



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Thwaites. 67-25 (BMNH).

Hiniduma (Gal. Dist.) -1a. Kanneliya Jungle, 500 ft, ii 11~12 1972, K.V. Krombein; -1b. viii 13~16 1972, K.V. Krombein and P.B. Karunaratne; -1c. i 11~16 1975, K.V. Krombein, P.B. Karunaratne, P. Fernando and N.V.J.A. Weragoda; -2. Kottawa Forest Reserve, iii 11 1972, K.V. Krombein and P.B. Karunaratne.

Kandy (Kan. Dist.)-1. Kandy Reservoir Jungle, iii 4 1972, K.V. Krombein and P. B. Karunaratne; -2. Udawattakele, x 1~3 1973, at black light, K.V. Krombein, P.B. Karunaratne and P. Fernando; -3. Kandy (Roseneath), iii 25 1971, P. and P. Spangler (Malaise trap); -4. Udawattakele Sanctuary, 2100 ft, viii 16~31 1976, S. Karunaratne; -5. Udawattakele, ix 2~9 1975, black light trap, D.M. Davies, S. Karunaratne and D.W. Balasooriya.

Peradenia (Kan. Dist.). Botanical Gardens, ii 13 1975, K.V. Krombein, P.B. Karunaratne, P. Fernando and S. Karunaratne.

Palutapana (Ham. Dist.). viii 10 1972, K.V. Krombein and P.B. Karunaratne.

Uggalkaltota (Rat. Dist.) -a. 350 ft, Irrigation bungalow, i 31 1970; -b. ii 8 1970; -c. 500 ft, x 10~14 1970, all D.S. Flint, Jr.

Sinharaja (Rat. Dist.). Sinharaja Forest, Weddagala, 1976, K.V. Krombein, P.B. Karunaratne and S. Karunaratne.

Wellawaya (Mon. Dist.). viii 10 1972, K.V. Krombein and P.B. Karunaratne.

Lahugala (Amp. Dist.) -a. Lahugala Sanctuary vi 13~14 1976, K.V. Krombein, P.B. Karunaratne and S. Karunaratne; -b. Lahugala, vi 15 1976, K.V. Krombein, P.B. Karunaratne and S. Karunaratne.

Explanation of Plate V

Fig. 1. *Trigona* (*Tetragonula*) *latigenalis* sp. nov. Worker.

Figs. 2-4. *T. (T.) laeviceps* Smith, respectively from Dai Lanh (Viet Nam), Karyu Danar (Viet Nam) and Pahang (Malaya), Workers.

Fig. 5. *T. (T.) fuscobalteata* Cameron, Worker.

Fig. 6. *T. (T.) iridipennis* Smith, Worker.

Fig. 7. *T. (T.) pagdeni* Schwarz, Worker. Figs. 1-7 shown in the same magnification.

Fig. 8. *T. (T.) zucchi* sp. nov. Nest entrance.

Addenda

After the completion of the manuscript, I had an opportunity to examine some males of "*T. iridipennis*" collected in India. These were similar to *T. iridipennis* from Sri Lanka in coloration, but their genitalia were, surprisingly, nearly identical with those of *T. pagdeni*. Thus, the name "*iridipennis*" should be restricted to the Sinhalese populations. For the Indian populations, the name *T. bengalensis* Cameron 1896 is tentatively proposed, which might differ only subspecifically from *T. pagdeni*. Detailed accounts will be given in a separate paper.